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WATER UTILIZATION BY TREES, WITH SPECIAL REFERENCE TO THE ECONOMIC FOREST SPECIES OF THE NORTH TEMPERATE ZONE

By

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CONTENTS

	Page
Introduction	1
Purpose and scope	1
General uses of water in trees	2
Absorption of water by trees	3
Water absorbed by shoots	3
Water absorbed by roots	3
Summary and suggestions for research	7
Storage of water in trees and water content of tissues	7
Water content of wood	7
Water content of leaves	10
Water content related to site	14
Summary and suggestions for research	15
Water losses of trees	16
Bleeding, guttation, and disposal of excess water	16
Water losses of trees—Continued.	
Water lost through transpiration	17
Summary and suggestions for research	58
"Adaptations" of trees to dry conditions	59
Methods of checking transpiration	62
Methods of assuring an adequate water supply	71
Testing ability of trees to withstand drought	73
Summary and suggestions for research	74
Water consumption by trees	75
Water requirement	79
Summary and suggestions for research	83
Literature cited	85

INTRODUCTION

PURPOSE AND SCOPE

During the last 50 years there has been an ever-increasing stream of literature dealing with the general water relations of plants. At one time the emphasis was placed upon water losses and at another on water absorption and the relation of the plant to the soil; in recent years the emphasis has been centered on the internal cellular changes associated with drought resistance. Most of this literature has dealt with herbaceous types both because of the ease with which such forms can be manipulated and studied under experimental conditions and because of the importance of this type of vegetation in the world's food supply and its consequent dominance in agriculture.

As the demand for water by industry, by agriculture in semiarid regions, and by expanding urban populations has increased, as the attention of students has been drawn by recurrent floods and excessive erosion to the relation between ground cover and the water regime of the soil, and as questions of the most efficient land utilization, reforestation of submarginal lands, and the general importance of timbered areas have come to be more appreciated, there has arisen a decided

need for a summary of present knowledge concerning the amounts of water utilized by our economic forest species and of the various problems associated with this utilization.

The following brief review of some of the problems involved and of the various contributions to their solution is here presented in the hope that students and workers will thus be able to obtain a general perspective of the field, of the present state of our progress, and of some of the problems still awaiting solution. Because of the size of this problem, however, it has been deemed advisable to limit the present discussion primarily to the tree itself. Problems associated with the relation of the trees to the water supply and with the factors outside the tree which determine the available supply, e. g., the soil complex, are, therefore, omitted in the following pages, in an attempt to focus the attention on (1) the amount of water the various tree species utilize and require during their growth and (2) the factors which determine this use of water. Only when these fundamental problems have been more completely studied will it be possible to take advantage of the known facts of climatology in their relation to optimum land productivity.

GENERAL USES OF WATER IN TREES

Water is without doubt one of the most important environmental factors influencing the life of trees. Trees will not grow except in the presence of at least a certain minimum quantity of water, depending upon the species; and, next to temperature, no factor plays so important a role in determining the distribution of the various tree species over the surface of the earth as does water. While the uses of water within the tree are manifold, they can be grouped into at least four major categories.

First of all, water enters into the composition of the dry matter of the tree. In the process of photosynthesis, carbon dioxide obtained from the air is combined with water obtained chiefly through the roots to form carbohydrates, according to the equation $6CO_2+6H_2O=C_6H_{12}O_6+6O_2$. Although this equation tells nothing of the intermediate steps or of the details of the process, it outlines the general scheme of the reactions and states the end products, which are sugars and oxygen. The sugars are built up later, with the elimination of water, into starch, and ultimately into cellulose, which makes up the bulk of the material in a tree, while the oxygen, in the economy of nature, is returned to the air.

According to this equation, since the molecular weight of water is 18 and that of sugar (glucose) is 180, it takes 108 g of water to make 180 g of carbohydrates; or, in other words, about 60 pounds (nearly a cubic foot) of water are required to make 100 pounds of dry matter. But since trees actually absorb about 300 pounds of water for each pound of dry matter manufactured, only about one-fifth of 1 percent of the water absorbed ever becomes incorporated into the substance of the tree.

While the use of water in the manufacture of food for the framework of a plant is its most important use to vegetation in general and to woody plants in particular, this is by no means the only function which water has in the tree. In order to carry on its normal functions, each living cell must contain enough water to keep the protoplasm in optimum condition and in contact with the cell wall. This requires a

definite degree of turgor in the cell, which means that the cell vacuoles must contain a minimum amount of water.

A third function of water in the tree is that of acting as a transporting medium. The minerals absorbed from the soil and needed by the stems and leaves, as well as the elaborated, organic foods manufactured in the aerial portions and required by the various organs and tissues of the tree, are all carried in water as the solvent medium.

Furthermore, water plays a part in practically all of the chemical reactions that take place within the cell. Tree organic chemistry, like most chemistry, is water chemistry, in which water either enters directly into the reactions or else is required as a solvent for the reactions to take place. Thus respiration, enzymatic processes, etc., all require the presence of water, which is thus seen to be of the highest importance in the life and growth of trees. The total amount of water utilized by a plant consequently depends upon (1) the amount absorbed, (2) the amount stored and used within the plant for the various purposes mentioned above, and (3) the amount lost in various ways.

ABSORPTION OF WATER BY TREES

The water the tree uses enters its immediate environment via the air and soil in the form of rain, snow, or other forms of precipitation. Before it can be of use within the tree, however, it must first be absorbed by the organism. This absorption process may take place, therefore, either through the aerial portions (the shoots) or through the subterranean portions (the root system).

WATER ABSORBED BY SHOOTS

Of the water absorbed, small quantities may be taken in by the leaves and branches during times of rainfall or from dew. Although the actual amount absorbed in this fashion by most plants is very small, dew may be extremely important in dry periods because of its effect upon the humidity and the consequent checking of water loss, and, according to Rubner (*178, p. 118*),[1] in dry summers it may serve as almost the sole source of moisture, especially for young plants.

WATER ABSORBED BY ROOTS

By far the greater proportion of the water absorbed by plants is taken in through the root system, the character of which for any given plant species depends upon a great many factors, including (1) the kind of soil, (2) the water content and distribution in the soil, (3) the amount and distribution of nutrients in the soil, (4) the aeration of the soil, and (5) the temperature of the soil.

SPECIFIC DIFFERENCES IN ROOT SYSTEMS

While these are the chief physicochemical factors in the environment determining the growth and form of root systems, two other important factors must be taken into account in any consideration of this subject, namely, the competition of other species and the inherent, hereditary characteristics of the plant, i. e., the so-called "specific differences" in root systems. Some trees, such as the pine, form tap-

[1] Italic numbers in parentheses refer to Literature Cited, p. 85.

roots and are thus able to reach deep-lying sources of water in the soil. Others, like the spruce, form a shallow system of fibrous roots which extend in all directions from the base of the tree, and which may, according to Bindseil (*15*), extend 30 feet from the base of the stem. Between these two extremes are all gradations and intermediate types.

The proportion of the root system to the rest of the tree also varies with the species as indicated by Bühler (*23*), who states that in 2-year-old spruce grown on loam soils in a nursery, the weight of the root system is 25 percent of that of the entire plant; in fir, 45 percent; in pine, 13 percent; in larch, 39 percent; while in the broad-leaved trees the root percentage is much higher, being 61 percent in the beech and about 76 percent in the oak. These specific differences in root systems are probably connected with specific water requirements.

These specific differences are considered by Hayes and Stoeckeler (*92*), who tabulate the relative rooting depths of trees 20 to 40 years old on fine-textured soils as follows:

Deep-rooted (10 to 20 feet in depth):
- Ponderosa pine.
- Hackberry.
- Honeylocust.
- Bur oak.
- Mulberry.
- Osage-orange.

Intermediate (5 to 10 feet in depth):
- Green ash.
- American elm.
- Red cedar.
- Russian-olive.
- Caragana.
- Boxelder.
- Black locust.

Shallow-rooted (1 to 5 feet in depth):
- Jack pine.
- Scotch pine.
- Norway spruce.
- White willow.
- Cottonwood.
- Catalpa.

EFFECT OF THE ENVIRONMENT

It is possible, however, for the environmental influences mentioned above, which include both the physicochemical and the biotic, or root-competition factors, to cause a pine to have a more widespreading root system than a spruce. Weaver and Kramer (*228*) have stated: "Although the root habits of a tree are governed, first of all, by the hereditary growth characters of the species, they are often quite as much the product of the environment."

Roots are living things and tend to grow through the soil in the direction of the materials needed for the life of the tree. Thus, if the soils are becoming dry, the roots tend to grow in the direction of available moisture; if a certain region is waterlogged and lacks air, the roots will grow toward better aerated regions; etc. The type of soil and its compactness also affect the type of root system developed in it, as pointed out by Hayes and Stoeckeler (*92*). The roots, in other words, show a certain type of "adaptation" to their environment within the hereditary mold. Some species, however, are much more plastic than others and are consequently able to grow in a greater variety of sites.

Although, according to Cheyney (*35*), jack pine, which grows in dry, sandy regions, is characterized by a widespreading shallow root system rather than by a deep-rooted system, as might be expected, in general seedlings that survive on more arid sites are more likely to possess a taproot at this early growth stage than seedlings of species growing in more mesophytic conditions, as discussed by Toumey (*215, pp. 157–165*). These same conclusions may be drawn from the work of Holch (*101*), who grew *Quercus macrocarpa* Michx., *Q. borealis* Michx., *Hicoria ovata* Britt., *Tilia americana* L., and *Juglans nigra* L. in three different habitats in southeastern Nebraska. The roots spread much farther than the tops and, in the species mentioned, produced during the first year root systems 5.7, 2.4, 2.5, 1.2, and 4.5 feet deep, respectively, the greater depth and stronger lateral branches being in the drier sites.

Somewhat similar results are reported by McQuilkin (*144*) for *Pinus rigida* Mill. and *P. echinata* Mill. in a fairly comprehensive series of studies on the root systems of these plants as influenced by age, site, type of soil, aeration, water supply, etc.

Not until much more information of this sort is at hand for all our economic species will our fundamental silvicultural practices be on a technically sound basis.

ROOT COMPETITION

The effect of root competition has been studied by numerous in vestigators, especially in the case of herbaceous plants. Craib (*39*) carried on some experiments to show the effect of this factor on the amount of soil moisture available to coniferous trees in New Hampshire. Trenches 1 foot wide and 3 feet deep were dug around white pines so as to isolate the soil from root competition of plants in the adjoining quadrats. The amount of available moisture was greatly increased by the elimination of root competition, and in very dry periods two to nine times as much moisture was available in the top 6 inches of soil in the trenched quadrats as in the untrenched. The competition comes largely from the herbaceous and shrub flora of the forest floor. Beech has about 50 percent of its roots in the top 35 cm of soil and spruce about 70 percent, according to Dengler (*46*), and most tree species have by far the major portion of their absorbing surfaces in the top 3 feet of soil. The effect of root competition by grasses and other herbaceous plants may, therefore, be very serious; in fact, the severity of the competition between grass roots and tree roots is considered by some authors (*169*) as the chief reason for the absence of trees on the prairies. Some trees, to be sure, have feeding roots 6 feet and more below the surface, but the proportion of roots at this depth is small.

In his well-known monograph on ecological relations of roots, Weaver (*226*) touches only incidentally on the root systems of trees, but in a later study (*227*) he performed an experiment to show the effect on young trees of competition with grasses. Honeylocust, boxelder, green ash, white elm, and silver maple were started from seed and grown for 3 years in the prairie near Lincoln, Nebr. Here grasses (mostly bluestems and *Panicum*) grow 3 to 6 feet high. Four different plots were prepared: In (1) the seedlings competed for water, nutrients, and light; in (2) they were watered; in (3) the grasses were clipped to destroy the light competition; and in (4) a strip of sod 1

foot wide was removed and the grasses kept out. In case (4) the competition was entirely removed and in (1) was complete. In (2) the water competition was accentuated; and in (3) the light competition was removed. All seedlings did best under (4), that is, when all of the competition of the grasses was eliminated. At the end of the third season, trees only 18 to 24 inches high had taproots 5 to 7 feet deep and surface roots almost as long. The mortality was much higher in the clipped area, showing the effect of the root competition, and still higher in the watered region, since watering promoted the grasses and increased the shade. In this case, (2), and also in (1), nearly all the seedlings succumbed, and those that did not were poorly developed both above and below ground.

Weaver and Kramer (*228*) studied the distribution of the roots of *Quercus macrocarpa* in the prairie in relation to soil type, root competition, and soil moisture content. They found that the taproot of this species may go down 14 feet but most of the thirty-odd branches of the taproot arose in the first 2 feet of soil. The main branches run out for 20 to 60 feet. The weight of the roots equalled that of the tops, and the volume of the roots was about 90 percent that of the tops. Water, it was concluded, was the determining factor in the form and extension of the root system.

Biswell (*16*) shows the relation between soil conditions in Nebraska and the root habits of seedlings and/or saplings of the following deciduous forest trees: *Gleditsia triacanthos* L., *Acer negundo* L., *Platanus occidentalis* L., *Juglans nigra*, *Aesculus glabra* Willd., *Quercus macrocarpa*, *Hicoria ovata*, *Acer saccharum* Marsh., and *Populus sargentii* Dode. Since the soils, moisture, etc., varied, no general conclusions are permitted except as to the possibilities of growth under these respective conditions. This paper, however, is one of the most recent on the root systems of North American forest trees.

The comparatively shallow nature of root systems and the competition offered by the herbaceous cover of the forest floor is further evidenced by the work of Pearson (*166*) who found that in ponderosa pine in Arizona roots seldom penetrated to a depth of 4 feet. Most of the taproots of the saplings studied were under 30 inches in length and the strongest laterals were within 1 foot of the surface.

That trees may absorb from deeper layers, however, is shown by the work of Shear and Stewart (*190*), who, in Illinois, found not only that larch, white oak, and white pine removed more water from the top 4 feet of soil during the growing season than did green ash and silver maple, but also that the white oak affected the water content of the soil to a depth of 10 feet, larch to 9 feet, silver maple and white pine to 8 feet, and green ash to 7 feet.

Among the other biotic factors influencing the absorption of water by trees should be mentioned the mycorhiza, filamentous fungi that attach themselves to the roots of trees. In some forms (endotrophic) they penetrate the cells of the root, while in other forms (ectotrophic) they are merely closely applied to the surface. Their relation to the trees is thought to be mutualistic rather than parasitic; while they doubtless use some of the elaborated foods stored in the root cells, they also are believed to supply soil minerals and water to the roots and thus function in the capacity of root hairs. These fungi, which are found especially in forest soils rich in organic nutrients, seem, in fact, to replace the root hairs in many forest species, and in the ab-

sence of such fungi the trees do not thrive so well, owing to some sort of inherited "adaptation" in the course of evolution. But this point has not yet been fully cleared up. At any rate, the mycorhiza, when present, apparently help the tree to absorb available moisture.

SUMMARY AND SUGGESTIONS FOR RESEARCH

Water is absorbed to a small extent by leaves and twigs but chiefly by the roots. The amount which they absorb depends not only upon the physicochemical nature of the soil and its moisture content but also upon inherent specific differences between plants and upon the biotic environment. This latter includes not only roots from other members of the same species but also those of the other species of plants in the same soil. In addition the role of micro-organisms and of mycorhiza must be considered. Although much yet needs to be done in determining the manner in which trees check transpiration, the role of roots in supplying water should not be overlooked. Under what conditions do the deep-lying roots function in supplying water and how effective are they?

While the broad outlines of these problems have been well understood for some time, we have little data of an intensive nature. In just what regions of the soil are the absorbing roots of the various species? Which layers of the soil are the most important for the water supply of individual species, and what adaptations are possible in the various tree species which will permit them to accommodate themselves to a changing soil-moisture content or to a falling ground-water level? To just what extent can environment change the genetic pattern of root systems, and to what degree is the inherited tendency of a species to form a taproot influenced by root mutilations, such as occur in transplanting nursery and other planting stock? Also what is the optimum spacing (density of stand) for the various soil-moisture conditions? And to what extent are range grasses and other minor vegetation such as chaparral and brush species compatible with trees and forests? In answering satisfactorily all these questions, much work still remains to be done.

STORAGE OF WATER IN TREES AND WATER CONTENT OF TISSUES

WATER CONTENT OF WOOD

Since water is passing from the roots to the leaves through the stems and branches, it is to be supposed that the stem tissue, although largely composed of dead cells, will, nevertheless, be rich in water.

The living cells of the wood parenchyma, cambium, rays, and phloem contain a certain amount of water in their vacuoles; but, in addition, one must consider the water content of the wood proper (especially the sapwood), as well as that of the pith and outer bark, since all of these tissues differ in their water content. The amount present also varies with the season, with the time of day, and with the species. Exact figures, taken mostly from European work, show that the average maximum is about 55 percent and the average minimum about 40 percent. The water content of a stem is determined by cutting it into pieces of equal size, weighing, drying at about 110° C., and

weighing again, the difference indicating the percentage of green weight.

R. Hartig (*87*) found that the water content varied between 30 and 60 percent in the 30 different species which he examined and in the same species at different seasons of the year; but if the curves showing the variation in water content of the various species throughout the year are compared, they show on the whole a marked parallelism. The highest water content occurs from December to March during the dormant period of the year and the lowest in June to September when the trees are most active. If a hardwood, such as the beech, is compared with a conifer, like the pine, it will be seen, however, that the water content of the beech sinks very much between July and October, while that of the pine sinks very little during this period. After the transpiration is diminished by the fall of the leaves, in the case of the beech, and by the onset of cooler weather, in the case of the pine, both trees show an increase in their water content which continues until the following spring. The same differences are seen if one compares spruce and oak.

Studies on this subject were also made by T. Hartig (*90*), who measured the water content of stems, roots, and leaves for 3- to 5-year-old trees of pine, spruce, oak, and beech. In the conifers the root and stem have a higher water content (61 to 64 percent) than the needles (49 to 51 percent), while in the hardwoods the roots contained 40 to 46 percent (of fresh weight) and the leaves about 50 percent.

Gibbs (*69*, *70*, *71*) studied the amount and distribution of water in *Betula papyrifera* Marsh., *Populus tremuloides* Michx., *Pinus banksiana* Lamb., *Picea glauca* Voss. (syn. *P. canadensis* B. S. P.), *Abies balsamea* Mill., and a few other species. He found more marked seasonal changes in the hardwoods than in the softwoods, and these changes, as might be expected, were more pronounced in the sapwood than in the heartwood. Daily changes, with a decrease in he forenoon and an increase later in the day, were also noted.

It is interesting to see, however, as is shown in table 1, that the twigs have the highest water content in the more active summer season rather than in the less active winter.[2]

TABLE 1.—*Seasonal water-content percentages in stem and twigs of birch, aspen, and pine* [1]

Month	Birch		Aspen		Pine	
	Stem	Twigs	Stem	Twigs	Stem	Twigs
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
November	41.39	32.73	49.1	33.5	50.0	48.3
December	42.39	44.4	51.0	49.3	61.9	51.2
January	45.59	44.4	50.0	47.5	62.7	56.1
February	46.23	42.7	50.5	50.2	61.3	53.7
March	44.8	39.2	49.6	46.2	58.5	61.3
June	38.1	51.3	42.2	50.5	55.2	60.1
July	41.3	49.9	41.6	50.8	52.0	60.2
August	39.1	44.8	42.7	53.1	55.1	56.6
September	38.4	38.7	41.3	46.0	50.5	52.3

[1] Figures from Tonkel, as reported by Büsgen and Münch (*33*, *p. 309*).

[2] For a history of the development of this subject and the variations in the moisture content of the wood in various parts of the tree and under the influence of various environmental factors, the reader is referred to Büsgen (*32*).

Friedrich (*60*) found that the water content of wood at about 6:15 p. m. was about 52 percent. Early the next morning it was about 56, and at noon on the same day about 51 percent. This difference of 5 percent between the water content in the early morning and at noon is explained by the water losses during the daytime, as will be discussed later. Doubtless the increase in the amount during the night serves to replenish the loss of the previous and following days. This effect may be important, since a 5-percent reduction of the water content of a stand running 100 M board feet to the acre would equal about one-seventh of an inch of rainfall, as calculated by Baker (*6*).

The moisture content of wood varies also with the height in the tree as indicated by Luxford (*141*), who noted that in redwood, especially in the heartwood, there was a marked decrease in the water content with height up to about 80 feet, when the decrease in water content became much more gradual. Sapwood, on the other hand, although containing much more water than the heartwood, seemed to increase only slightly in water content at the higher levels, the net result being a decrease of about 15 percent per entire cross section between the top and bottom of the tree. Huckenpahler (*111*), however, working with shortleaf pine in North Carolina, found that the moisture content in an entire cross section (in summer) increased upwards from about 80 percent of the dry weight at 1 foot above the ground to about 175 percent at 25 feet. The water content of the phloem changed very little with height, but the wood, especially the sapwood (outer two rings) increased from 100 percent at the 1-foot level to 185 percent at the 25-foot level. Both workers are agreed, however, on the fact that the heartwood decreases decidedly in water content from the base upward. The total amount of water in a tree may thus reach a very large figure; in a redwood 5 feet in diameter and 200 feet high Luxford calculated that there are about 17 tons of water.

Drought periods are reflected in the moisture content of the wood, as shown by Beilmann (*12*), who found that in the vicinity of St. Louis the unusual seasonal distribution of the rainfall in 1932–34 ultimately resulted in severe wilting or total defoliation in July 1934, accompanied by changes in the wood-moisture content, as measured in borings from about 25 different species. The moisture content averaged about 50 percent of the wood. The higher the water content the better were the trees. Those trees with less than 50-percent moisture content (July 19–22, 1934) were either seriously wilted or completely defoliated. In agreement with other workers Beilmann (*12*) found that trees of similar apparent condition may vary as much as 5 percent in their wood-moisture content.

OSMOTIC PRESSURE MEASUREMENTS

In the studies just described, the water content has been measured on a dry- or fresh-weight basis. In the living cells of the tree, water content is important, however, not only from the point of view of absolute amounts present, but also from the point of view of the proportion of osmotically active substances that the cell sap may contain in solution. This determines the osmotic pressure of the cell, which, in turn, determines the ability of the cell to take in water from the outside or to pass it on to other cells. Numerous studies have been

made on the osmotic pressure of the cells of trees, and any discussion of the water relations of trees must consider this phase of the subject.

Since the freezing point of a liquid varies with its osmotic value, the determination of the freezing point of plant saps and juices is a common method of determining the osmotic value of the plant liquids. Thus Dixon and Atkins (*49*, *51*) measured the osmotic value of sap that had been centrifuged from the sapwood of trees and obtained the following results for *Ulmus campestris* L. on March 4, showing that the osmotic value varies with the height in the tree:

Height above the ground (meters):	*Osmotic pressure (in atmospheres)*
0.6	1. 13
16.0	2. 09
20.0	3. 52

Similar results showing both the effect of the height in the tree and of the season are given in table 2 for *Acer macrophyllum* Pursh.

TABLE 2.—*Variation in osmotic pressure with height in tree and season*

Height (meters)	Osmotic pressure			Height (meters)	Osmotic pressure		
	Oct. 13	Feb. 25	Apr. 14		Oct. 13	Feb. 25	Apr. 14
	Atmospheres	*Atmospheres*	*Atmospheres*		*Atmospheres*	*Atmospheres*	*Atmospheres*
Root	0. 72	1. 07	1. 34	Stem at—Con.			
Stem at—				6.0	.49	2. 15	1. 73
Ground	.63	1. 76	1. 31	8.0	.57	2. 70	1. 98
2.0	.56	1. 76	1. 30	10.0	.81	3. 71	2. 16
4.0	.42	2. 14	1. 30				

Similar results were obtained also with *Cotoneaster frigida* Wall., *Ilex aquifolium* L., and other species, although the osmotic pressure was found to vary somewhat with the species. The sap was centrifuged from the sapwood, but the centrifuging force is not given. The authors, however, call attention to the amount of liquid that can be obtained in this fashion and state that in December a piece of *Salix babylonica* L. wood 2 cm in diameter and 10 cm long gave as much as 4 cc of water, although a yield of 1 to 2.5 cc was the usual amount for pieces this size.

These workers were among the first to note the gradient of the osmotic pressure in the cells of the wood as height above the ground increases. The importance of this for the ascent of sap and the life processes of trees will be discussed further in the following section.

WATER CONTENT OF LEAVES

Since the cause of the ascent of sap in trees is very complicated and lies somewhat outside the scope of this work, it will be touched upon only very briefly in connection with the other problems involved. Briefly, Dixon and his coworkers have shown that the water is pulled up the tree by the leaves during transpiration, radiation (from the sun) supplying the necessary energy. As the water evaporates from the living cells of the leaf, more water is drawn in from the tracheids and other conducting cells in the leaves, stems, and roots, aided chiefly

by the action of the living cells in the root tissues. The chief contribution of these workers was in showing that the tensile strength of the water column was sufficient to permit the columns of water to be lifted the distance required in the tallest trees. While the energy for this process comes ultimately from the sun, other forces are thus seen to come into action, including those of surface tension, osmotic pressure, root pressure, etc. It is consequently natural to expect to find an osmotic gradient in plants as one goes upward from the soil. Since the active force required to extract water from a living cell (e. g., by evaporation) and the force required to add water to that cell from tissues below depends largely upon the osmotic forces active in the cell, such an osmotic gradient from roots to crown may be anticipated.

Ewart (*58*) was one of the first to show that the osmotic pressure of leaves increased with their elevation on the tree, but at this early period he thought that the sources of error in the methods then available were too great to permit any conclusions, since he got equally great differences between leaves at the same level or with leaves of different ages. It has later been found, however, that while the difference in position is not the only factor bringing about differences in osmotic pressure, there is in general a difference in the osmotic pressure of leaves at different levels on the stem, other factors being equal. This was shown by Dixon and Atkins (*48*) who obtained differences in osmotic pressure in *Magnolia*, *Fraxinus*, and *Ulmus* leaves from various levels in the tree; but they also got very varied results and came to no general conclusions. Part of their difficulty lay in the fact that the tissues were not given the preliminary freezing treatment which they later found to be necessary.

Harris, Gortner, and Lawrence (*85*), in their fairly complete series of studies on this subject, showed very clearly that there was a distinct difference in the osmotic concentration of leaf sap at different elevations on the tree. They measured 26 trees of 12 different species and found that the osmotic pressure without exception increased from lower to higher levels. Results from *Quercus prinus* L. are typical:

Height (feet):	*Osmotic pressure (in atmospheres)*
47	20. 23
36	20. 08
30	19. 72
19	19. 57

These differences in osmotic pressure are considered as due chiefly to carbohydrates, since the concentration of electrolytes commonly decreased upward. In a later paper (*86*) these authors found that sap of trees and shrubs consistently shows a higher osmotic pressure than that of herbs in the same environment. The sap of 19 species of trees from Long Island had an average Δ (depression of the freezing point) of 1.29° C.; that of 36 shrubs from the same section had an average Δ of 1.18°; and that of 162 herbs from the same locality had a Δ of 0.85°. Similar work carried on in the deserts of Arizona and in the rain forests of Jamaica showed similar differences between trees, shrubs, and herbs, the osmotic pressure in these different localities being 26.47 to 38.63 percent more in the cell sap of the trees and shrubs than in that of the herbs. Here again is noted an increase in osmotic pressure in trees with distance above the ground. Since the appearance of these papers of Harris and his associates this increase

in osmotic pressure with elevation above the ground has never been seriously questioned.

Later workers in this field have done little but accumulate supporting evidence from other trees and types of plants. Thus Regli (*174*) reports that in *Fraxinus excelsior* L. and *Pyrus communis* L. the higher above the ground the leaves are attached the higher is the osmotic pressure. This is also true for vines like *Aristolochia* and *Hedera*; and in compound leaves (*Fraxinus* and *Robinia*) it was found that there is even a progressive increase in the osmotic pressure of the leaflets from the base to the tip of the leaf. Huber (*107*) goes so far as to divide the tree crown into zones of iso-osmotic pressure and on this basis explains the dying back of the tips of branches in dry weather; since the tips are farthest from the supply, they are the first to feel the effects of drought.

SEASONAL VARIATIONS AND RELATION TO HARDINESS

Seasonal variations in the osmotic pressure of the cell sap of trees have been the object of considerable study. Dixon and Atkins (*50*) were among the first workers in this field also. They found higher osmotic pressure in lilac and holly roots and leaves in the winter; in the case of leaves this was attributed to an increase in electrolytes, but in the case of roots to an increase in carbohydrates.

Lewis and Tuttle (*135*) found a maximum osmotic pressure in leaves of evergreens in March; this was followed by a sudden decrease, which they considered was associated with a decrease in sugar content brought about by the increased temperatures of spring. These workers, as well as others, associated the increased osmotic pressure of plant cells in winter with their increased hardiness, and showed (*136*) that the osmotic pressure of the sap of *Picea glauca* needles near Edmonton, Alberta, dropped from 20 atmospheres in late April or May to 16 or 17 atmospheres as the leaves passed into the summer condition. These changes seemed to be quite independent of altitude and were found in other trees, such as *Picea engelmanni* (Parry) Engelm., *Pinus albicaulis* Engelm., *P. contorta* Dougl. (syn. *P. Murrayana* Balf.), etc., which grow at various altitudes.

Goldsmith and Smith (*72*) showed that the water content (based on fresh weight) of the leaves of *Picea engelmanni* at four typical stations throughout the altitudinal range of this tree (6,500–11,500 feet) in the Pike's Peak section, was relatively high (60–80 percent) in late spring, falling rapidly to a summer level and then slowly diminishing in winter to 50–56 percent. The osmotic pressure changed in a reverse fashion, being lower in summer and at a maximum in April or May.

Gail (*63*) found somewhat similar results in various conifers in the northwestern United States. In *Pinus ponderosa* Dougl. the osmotic pressure was highest in midwinter and least at the end of June and early July. Gail found also that the osmotic pressure increased with the altitude. When sudden cold spells occurred, the plants did not have a chance to increase the osmotic pressure by changing materials that are not osmotically active, such as starches, into osmotically active substances, such as sugars, and under these circumstances the plants were sometimes killed. That the high osmotic pressures are due to soluble carbohydrates is indicated by the fact that when the food-manufacturing tissues—the leaves—stopped functioning or

dropped, the osmotic pressure very suddenly decreased from 26.53 atmospheres to 8.43 in *Larix occidentalis* Nutt. and from 19.5 to 5.4 atmospheres in *Fraxinus pennsylvanica lanceolata* Sarg.

So many workers have shown the relationship between osmotic pressure and hardiness in herbs, as well as in shrubs and trees, that the connection between these two phenomena can hardly be questioned. Meyer (*151*), however, believes that other factors besides osmotic pressure must be taken into account. He finds the water content of the needles of *Pinus rigida* highest in summer and lowest in late spring and admits that the maximum osmotic pressure (25.73 atmospheres) occurs in January, but he thinks the differences in osmotic pressure are not sufficient to explain the hardiness of this species, which he attributes to the presence of pentosans and water-holding colloids. In a later paper (*152*) he records that the total amount of water in needles of this species was about 5 percent less in winter than in summer, with a corresponding difference in osmotic pressure.

The research in this field indicates, in general, that the total water content of leaves is higher in summer than in winter, when there is not only a lower absolute water content but also a lower relative water content, inasmuch as the water at this time contains a greater percentage of soluble materials.

OTHER FACTORS INFLUENCING WATER CONTENT OF LEAVES

Furthermore, the water content of leaves varies not only with the season but also with the local climatic factors, age of leaf, etc. Härdtl (*84*) showed that the water content in the blade and petiole varies with the developmental stage of the leaf, and as the cell walls increase in thickness this change in water content is associated with the torsion stresses which help to maintain the leaf in its proper position.

Other workers have emphasized the water content of leaves in relation to wilting. Schröder (*182*), for example, who studied the water loss of detached leaves over a period of time in order to observe the maximum amount of water which the leaves could lose and still recover when placed in water, found the relative water content of leaves to be as follows, in percent: *Fagus* 50.5, *Prunus* 56, *Pinus* 56, *Salix* 58, *Quercus* 59, *Acer* 63, *Platanus* 63. *Alnus* 63, *Aesculus* 66, *Betula* 59, *Tilia* 61.

Since these figures are obtained from drying in the air and hence do not include the chemically and hygroscopically bound water, they are somewhat smaller (but not much) than those reported by Ebermayer (*56*), who gives the following average water content of fresh leaves:

	Water content (percent)
Lombardy poplar	70. 49
Ash, horse chestnut	65. 90
Black alder, black locust	64. 10
Oak, elm, white alder, linden	63. 32
Birch, mountain ash, sycamore	61. 66
Willow, Norway maple, aspen	69. 48
Beech, hornbeam, field maple, white poplar	57. 02

These figures also agree essentially with those of Clark (*36*), who found in *Populus* leaves a water content of about 60 percent. This student also noted only very slight changes in the water content of leaves during the course of the day, but did find that the content varied somewhat with the season.

Schröder also studied the water content of leaves during wilting and dying, as well as the changes in the leaf structure at this critical period. The first portions of the plant to suffer are generally the margins or tips of the leaves and then the parenchyma regions between the main veins, in other words, the regions most remote from the water supply. Death occurred when the water supply was reduced to the percentages shown in table 3.

TABLE 3.—*Percents of water content of leaves at time of death*

Genus	Percent of normal water content	Percent of fresh weight	Genus	Percent of normal water content	Percent of fresh weight
Betula	75	45	*Platanus*	48	30
Alnus	74	46	*Aesculus*	46	30
Fagus	70	35	*Tilia*	82	50

The water content of both leaves and twigs of 11 evergreen and 11 deciduous species including *Picea excelsa* Link., *Carpinus betulus* L., *Pseudotsuga taxifolia* (Lamb.) Britt., *Pinus strobus*, *Fagus sylvatica* L., *Betula verrucosa* Ehrh., *Quercus robur* L., *Acer platanoides* L., and *Ulmus campestris* from the botanical garden at Sophia, were studied by Stefanoff (*207*). The "water capacity" was measured by the difference between the weight after standing in water under glass jars 48 to 72 hours and the weight after drying for 7 hours at 105° C. The "water content" was the difference between the fresh and dry weights, and the "water deficit" the difference between the water capacity and the content. Measurements were made in the morning and in the afternoon from March to September in the conifers, and from April to September in the deciduous species. It was found that the water capacity, which varied with the age and structure of the leaves and twigs, was highest in the deciduous species in May and in evergreens in June. The maximum capacity was about the same for all species (70 to 80 percent of the dry weight). The deciduous species decreased more rapidly with age than the evergreens. Actual water content, which was always less than the capacity and varied not only with the species (especially with the internal conductive tissues) but also somewhat with the soil moisture, temperature, humidity, etc., was usually greater in the morning than in the afternoon, and was less in June and July. The deficit exceeded 10 percent in only a few species at any time, the maximum being about 16 percent with *Thuja orientalis* L.

WATER CONTENT RELATED TO SITE

Since the density of the cell sap (that is, osmotic pressure) may be a measure of a plant's ability to absorb water from the tissues below it and ultimately from the soil itself, Korstian (*129*) tried to correlate the osmotic pressure in leaves with site conditions in the Wasatch Mountains of Utah, where he studied the freezing-point depression (Δ) of the cell sap of leaves of a number of tree species. The osmotic pressure of the leaves increased in winter, and the more drought-resistant species generally had higher sap concentrations. Consequently, the more favorable the site, especially from the point of

view of moisture, the lower, by and large, was the sap concentration. Korstian also found that cell sap of trees had a higher osmotic pressure than that of herbs and that the osmotic pressure was higher in the sap of leaves than in that of the roots. In *Pinus ponderosa*, for example, the osmotic pressure of the leaves was 16.2 atmospheres in July and that of the roots 12.4 atmospheres. Similarly, 2-year-old leaves (average of 10 trees) showed an osmotic pressure at the base of the crown of 17.3 atmospheres, while at the top of the crown, 40 feet above the ground, the osmotic pressure was 18.5 atmospheres. The second-year leaves had a consistently higher osmotic pressure than the first-year leaves, but these latter also show distinct differences with age as shown in table 4.

TABLE 4.—*Variation in osmotic pressure with age of needles in four species of pine*

Species	Osmotic pressure in—	
	1-month-old needles	1-year-old needless
	Atmospheres	*Atmospheres*
Pinus ponderosa Dougl	16.7	18.6
P. ponderosa scopulorum Engelm	17.6	18.9
P. contorta Dougl	15.5	17.1
P. monticola Dougl	12.9	17.0

Korstian also found that the osmotic pressure of the sap of colored leaves at time of leaf fall was always less than that of green leaves, which agrees with the results of Gail (*63*) mentioned above; he gives the following figures:

	Osmotic pressure (in atmospheres)
Populus tremuloides Michx.:	
Yellow leaves	16.7
Green leaves	22.0
Acer grandidentatum Nutt.:	
Red leaves	17.3
Green leaves	18.3
Prunus melanocarpa Shafer:	
Red and yellow leaves	15.4
Green leaves	21.0

Similar correlations between osmotic pressure and site factors are reported by Regli (*174*) and also by Walter (*224*) in his excellent monograph on water relations ("Hydratur") of plants with special reference to osmotic pressure and drought resistance.

In more recent work with *Covillea tridentata* Vail, Mallery (*146*) has attempted to correlate the osmotic value (Δ) of expressed sap from leaves and twigs of this xerophytic shrub with various environmental factors. It was found that the osmotic value of the expressed sap varied with the rainfall and soil moisture more than with soil type or salt content of soil. Osmotic values were always highest at the end of the dry season and lowest at the end of the rainy season and thus might serve as a moderately good index to the available water supply.

SUMMARY AND SUGGESTIONS FOR RESEARCH

While the chief function of the stems and leaves is transportation of water and manufacture of food, respectively, they also (especially the stems) store varying amounts of water. This is reflected in the

osmotic pressure of the cell contents, with the result that there is an osmotic gradient between the roots and the leaves, the osmotic pressure increasing upward. Whatever makes for water depletion apparently tends to increase the osmotic pressure in the cells and vice versa. The extent to which the osmotic pressure may be taken as an index to the site conditions has been studied by several workers, but much here still remains to be done. To what extent can trees use stored water to tide them over unfavorable conditions? And under what conditions and on what sites will maximum storage result? What use, if any, do trees make of this stored water in reproduction? And does the water content of trees during heavy seed years differ markedly from that during years when few seeds are produced? What effect do changes in the ground-water level, precipitation, etc., have upon this storage of water, and how is this related to the subsequent drought resistance? And, above all, how can a knowledge of these principles be applied to the practical business of silviculture and watershed management? The answers to all these questions await the developments of future research.

WATER LOSSES OF TREES

As has just been indicated, both the amount of water absorbed by plants and the amount stored by them depend to a very large extent upon the amount lost. These water losses occur through (1) bleeding, (2) guttation, and (3) transpiration.

BLEEDING, GUTTATION, AND DISPOSAL OF EXCESS WATER

Bleeding is the loss of water (with any included dissolved materials) from cut ends of stems and branches. It is a result of the root pressure below, which apparently forces water up the stem whether or not it is being used by the parts above. Some plants bleed much more readily than others. Thus Hartig (*87*) noted that maples and birches bleed more easily than most other trees, followed by beech and hornbeam. The cut surface becomes distinctly wet in black locust, willows, alders, poplars, firs, and larches; but not even a wetting of the surface can be observed in pine, spruce, oak, horsechestnut, and basswood. Since bleeding occurs only under abnormal or accidental conditions, it need be discussed no further at this point.

Guttation, by which is meant the secretion of water through leaf scars or special glands in the leaves, likewise plays a very minor role in trees of the temperate zones. Although in warm, humid climates, such as that of Louisiana, guttation is very marked in the autumn through leaf scars in some deciduous trees, e. g., the hackberry, it is chiefly of importance in tropical rain forests and, in general, is not especially noticeable in the region under consideration in this publication.

In the Tropics, where there is a great excess of moisture, leaves very frequently have structures which permit or even favor the rapid run-off of rainwater. Since drops of water remaining on the leaf epidermis frequently act like convex lenses and may result in local burned areas, it is advantageous in bright sunlight for the leaf to rid itself of surface films and drops. Many plants in the Tropics droop and thus permit the rain to run off quickly; and prolonged tips or

"drip points", as in *Ficus religiosa* L., aid in this process. Other reasons why the leaf should be freed from rainwater as quickly as possible are that its presence favors the establishment of parasites and also the film of water checks normal transpiration and metabolism. Although drip points are associated chiefly with climates of high rainfall, some trees in temperate climates, e. g., species of *Betula*, *Populus*, and *Alnus*, are provided with these structures.

The draining of water from the crowns of trees in the Temperate Zone generally proceeds either centrifugally, as in the linden, where the water runs off the edge of the tree first, or centripetally, as in the beech, where the water from the leaves passes first to the branches and thence to the main stem, from which it passes to the ground.

WATER LOST THROUGH TRANSPIRATION

By far the greatest losses of water occur through transpiration, by which is ordinarily meant the losses through evaporation from the leaves. Van Tieghem (*218*) originally used the term for the loss of water from the tissues that did not contain chlorophyll and reserved the term "chlorovaporisation" for the loss of water from the cells with chlorophyll. But neither these distinctions nor those of Henslow (*94*), who distinguished between transpiration from the protoplasm and that from the chlorophyll, have been maintained in recent work; and the term "transpiration" is now used to include all water losses from the leaf tissues.

The distinction between cuticular and stomatal transpiration of Von Höhnel (*97*) is still held, however, the former being the water lost from the epidermal cells of the leaf while the latter is that from the internal cells through the stomata. In addition, Buscalioni and Pollacci (*31*) have designated as "stomato-cuticular transpiration" that water lost from the surface of the guard cells, but this seems to be a rather fine point and has not been considered very seriously by later workers.

The term "specific transpiration" is also in use and refers to the percentage of water in a leafy twig that is lost in a unit of time. Thus, if the water content of a fresh shoot is 63 percent and if the water loss during a given period were 9 percent, the specific transpiration as used by Neger and Lakon (*161*) would be $\frac{9\times100}{63}$ or 14.3.

By "absolute transpiration" is meant the loss of water in mass units from a given tissue, while the term "relative transpiration" was introduced by Livingston (*138*) to mean the ratio of the transpiration rate per unit of leaf surface to the evaporation rate per unit of water surface, as measured with the "atmometers" devised by him. These are porous clay structures connected with a water supply permitting free evaporation from their surfaces. Inasmuch as the leaf is a living structure and, therefore, exercises some control over the water losses, evaporation from the leaf is generally less than that from the atmometer. A comparison of water losses from equal areas of leaf surface and atmometer surface gives one, therefore, the relative transpiration. This term, "relative transpiration", occurs very frequently in the literature and should be well understood by a student of this subject.

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The relative transpiration (frequently called also the "transpiration capacity" or "transpiring power") is a very valuable concept in botanical science, since it enables one to form an idea of the combined effect of the factors which influence the transpiration rate as modified both by external conditions and by the internal anatomical structure of the plant. For instance, if the mean transpiration capacity, during the day, of *Betula* is 0.59, of *Quercus* 0.16, and of *Pinus* 0.06, these figures serve to indicate the relative protection against water loss possessed by these three plants, as pointed out by Huber (*106*).

The subject of transpiration has been studied more than any other phase of water relations. Most of the experiments, to be sure, have been carried on with herbaceous plants, but there is little reason to doubt that the principles of transpiration hold throughout the plant kingdom, whether one is dealing with herbaceous or woody forms. In the following pages the subject will be reviewed very briefly with special reference to the literature on trees, in order that the reader may form a fairly adequate concept of the work that has been done in this field and of the organization of the subject; but for more detailed summaries he is referred to Burgerstein (*28*) and the more recent work of Seybold (*189*). A part of this literature has been reviewed also by Maximov (*148*), but he has been interested primarily in soil-moisture studies with special reference to plants of dry climates, and for this reason this last-named work is not so comprehensive as the monographs of Burgerstein and Seybold. It might also be mentioned that Seybold has not duplicated the field covered by Burgerstein, who devoted himself largely to the older and more classical phases of transpiration, in that he studied largely the factors influencing transpiration and the methods by which plants check transpiration. Seybold, on the other hand, has considered the question more from the point of view of the recent developments in physics and chemistry. The two monographs, therefore, supplement rather than duplicate each other. While both Burgerstein and Maximov devoted some attention to the ecological aspects of the question, these phases are developed much more fully by Seybold.

METHODS OF STUDYING TRANSPIRATION

The methods of studying transpiration may be outlined as follows:

I. Determination of amount of water absorbed by the plant to compensate for that lost by transpiration—potometers and lysimeters.
II. Measurement of stomatal openings.
III. Collection or determination of the water vapor transpired.
  a. Collecting the moisture given off with a hygroscopic substance, such as P_2O_5 or H_2SO_4.
  b. Measuring the change in humidity of the surrounding atmosphere with a hygrometer.
  c. Using some sort of "indicator" applied to the leaf.
    1. Cobalt chloride paper.
    2. Collodion.
IV. Determination of changes in weight of the plant due to loss of water.
  a. Using cut parts.
  b. Using entire parts.

Methods I and II are both indirect, inasmuch as they do not consider the actual water losses. Method I—the determination of the water absorbed by the plant—can be only a rough approximation, since all of the water absorbed is not lost; part is utilized for the various purposes to which water is put and which were discussed at the beginning

of this paper. This is well illustrated by the results of Eberdt (*53*), who reports the following differences between the intake and output of the sunflower (table 5).

TABLE 5.—*Water intake and output of sunflower leaves in 12 hours*

Observation period	Water intake	Water output	Difference
	Grams	*Grams*	*Percent*
7:15–8:45	16.67	15.55	+7
8:45–11:45	4.95	5.53	−11
11:45–3:00	5.50	7.40	−26
3:00–7:15	6.45	5.50	+15
Total in 12 hours	33.57	33.98	−1

Potometers consist essentially of a vessel of water arranged in such a fashion that it is possible to measure amounts removed by a plant inserted in the vessel. They are extremely easy to manipulate, and various types are on the market. Some of the more recent devices register automatically the water losses from the vessel.

Lysimeters differ from potometers in that they contain soil and thus provide a more natural environment than do potometers, but experiments with lysimeters, like those with potometers, do not permit one to distinguish between the water used within the plant and that lost or wasted. Furthermore, in such experiments it is very difficult to control and limit the water supply without interfering with some other function or phase of metabolism such as aeration (respiration), root expansion, or mineral nutrition. Therefore work with lysimeters requires a rather elaborate system of controls, if it is to be helpful in general silvicultural practices.

Collecting water vapor with a hygroscopic substance, such as P_2O_5 or H_2SO_4 (method III, *a*), is a fairly easy procedure. The substance is weighed carefully before and after, the difference in weight being the amount of water given off by the plant organs. This method, however, has a very serious weakness, inasmuch as the transpiration necessarily occurs in a space with an abnormally low humidity. It is thus quite unsuitable for measuring transpiration under normal conditions.

Minckler (*153*) has attempted to overcome some of the weaknesses in this method so that it can be used more successfully for field work with trees. By using more "active" drying agents, such as anhydrous magnesium perchlorate and barium perchlorate, distinct results can be obtained during 6 minutes. While it is true that the leaves during this time are probably not influenced much by the enclosure, provided the temperature and quality of irradiation are not appreciably changed, they probably do transpire differently from what they would in an open environment with a natural (and not an experimentally low) humidity. Also it must be admitted that, since the age, exposure, etc., all influence the transpiration of leaves on any given twig, as will be shown in the following pages, calculations on the transpiration of a tree based on any one of its twigs under such an environment will not be very trustworthy.

Measuring the changes in humidity with a hygrometer (method III, *b*) is much more satisfactory, but the objection to this is that it also is

carried on in a closed container, so that the humidity is constantly increasing.

The cobalt chloride method, which has been in use for many years but which was revised and standardized by Livingston and his coworkers, depends essentially upon the change in color of cobalt chloride with change in moisture content. Strips of paper impregnated with the salt are applied to the leaf surface and the rate of change of color is taken as an index to the transpiring rate of the plant. This method, which is thus seen to be qualitative rather than quantitative, in contrast with the two methods just described, is now used by a great many workers to compare relative rates of water loss. The collodion method is similar and depends upon the fact that collodion loses its transparency and becomes cloudy when a very small amount of water comes in contact with it. In using this method a solution of collodion in alcohol or ether is applied with a brush in a thin layer to the surface of the leaf. Very shortly the solvent evaporates, leaving a dry film of collodion. As transpiration proceeds, the collodion absorbs water, and the rate of clouding indicates the transpiration rate.

By far the best method is the direct determination of water loss by noting the change in weight of the plant (method IV). This may be done by comparing parts of plants or by using the entire plant, but the latter method is by far the more reliable and should be used wherever possible. With detached organs the experiment must be limited to a few hours or days, and there is no question but that enormous errors have arisen in transferring the data from cut parts to whole plants (as will be shown under the discussion on water requirements), but the difficulty of using large plants such as trees is obvious.

Furthermore the cutting of a leaf or twig from a plant, even though the cut is made under water and the plant part is then left in water, changes the transpiration rate. Although Bartholomew (*10*) found that when citrus leaves were cut they lost less water than before, most observers report the contrary, which seems more natural to expect. When attached to the plant, leaves are seldom transpiring at a maximum because of an insufficient water supply and because of the energy required to absorb water through the tissues between the leaf and the soil. When cut and placed in water these hindrances disappear. Thus Kamp (*119*) found in studying 30 species of woody plants that, when the leaves were cut, they transpired up to 130 percent more for the first 15 minutes than before cutting, after which the transpiration rate gradually decreased to its former level. Palladin, as recorded by Molliard (*157, p. 242*), likewise found that one detached oak leaf transpired 3.2 g in 24 hours while a twig of the same plant with 180 leaves lost only 28.2 g in the same period. The transpiration of the isolated leaf was thus 20 times that of the others. The reason for these changes is not clearly understood. If the leaves are really freed from previous stresses, why does the transpiration later decrease to normal instead of continuing at the maximum? Changes at the cut surface as well as in the size of the stomatal openings and in the suction forces involved probably play a role in these phenomena, but this entire question needs further study.

FACTORS INFLUENCING TRANSPIRATION

The factors influencing transpiration are either external (light, temperature, etc.), depending upon the environment, or internal and connected with the inherent nature of the plant.

INTERNAL FACTORS

Number and Location of Stomata

Among these internal factors, to be mentioned first of all are the number and location of the stomata. Since the stomata are openings in the epidermis through which the moisture from the inner cells of the leaf can escape, it is to be expected that, other things being equal, leaves or regions with more stomata will show more transpiration. Not all of the water, however, evaporates through the stomata; it has been estimated by Haberlandt (*81*) that about 10 percent of the total water lost from leaves is through the cuticle. These figures differ from species to species, since the percentage of the area taken up by the stomata also differs. In the horsechestnut it is estimated that the proportion of water transpired by the cuticle to the total evaporation of the leaf is as 1 is to 7.6, and in the birch as 1 is to 10.6.

The stomata are located for the most part on the under side of the leaves, although leaves of some trees contain stomata on both sides. Some maple species have stomata only on the under side but a few have stomata also on the upper side, according to Warsow (*225*). In *Tilia grandifolia* Ehrh., *Fraxinus excelsior*, and *Acer pseudoplatanus* L. they are most plentiful in the center of the lower side of the leaf, diminishing towards the margin. In these species stomata are completely absent from the upper side, as is also the case in *T. europea* L. and *T. silvestris* Desf. In conifers the stomata appear as white points in longitudinal rows on the needles. In the silver fir they occur only on the under side; but in *Pinus strobus* and in certain species of *Thuja* and *Juniperus*, they are found only on the upper side. Out of 1,359 species of broad-leaved trees studied by Koehne (*126*), stomata were found on the upper side of the leaves in only 222 species. The following average numbers of stomata per square millimeter of leaf surface were found by Espe (*57*) on the under side of leaves:

	Number
Fraxinus	494
Aesculus	318
Tilia grandifolia Ehrh	222
Prunus avium L	203
Juglans regia L	195
Acer pseudoplatanus L	112
Malus malus Britt	106
Prunus laurocerasus L	76

Oaks have an unusually large number of stomata, varying in different species, according to Yocum (*246*), from about 500 to 1,200 per square millimeter. This seems somewhat surprising in view of the comparative drought resistance of oaks, and indicates that number of stomata alone is not a determining factor in transpiration. This is supported further by his findings that on a sprout which grew 44 inches during one season the number of stomata increased from 410 per square millimeter at 8 inches above the ground to 533 at 40 inches. All were mature leaves, indicating that it is possible, under certain conditions, for the number of stomata to vary directly with the drought resistance rather than inversely, as is usually the case in trees. This question, however, like many others, needs much further study.

Also most workers are agreed that, in general, leaves transpire more from the side possessing the greater number of stomata, but so

many other factors have to be taken into account that the relation becomes no longer a direct one. In *Tilia europea*, in which the upper side contains no stomata, only two-sevenths of the water loss occurs through this side of the leaves, but this is probably a higher proportion than in most trees. Thus in *Citrus* species Bartholomew (*10*) found 85 to 95 percent of the transpiration was from the lower surface where the stomata are located, while Haas and Halma (*78*) found that two to three and one-half times as much water was lost through the under surface as the upper; and according to Haberlandt (*81*) the cuticular transpiration is only one seventy-sixth of the total in *Aesculus hippocastanum* L., one eighty-first in *Corylus avellana* L., and about one-eleventh in *Pyrus communis*. Even cutinized epidermis is not completely impermeable to water.

Age of Leaves

The age of leaves likewise causes a change in their transpiration activity. Von Höhnel (*97*) cut the leaves from shoots of *Tilia* and *Ulmus*, placed them in water, and followed the course of subsequent transpiration by weighing. The youngest leaves transpired the most, and as the leaves matured the evaporation gradually diminshed; but later a second maximum was reached when the leaves were completely developed. He explained this by assuming that in the youngest stage only cuticular transpiration was present; and since the cuticle and epidermal walls are very tender the transpiration was accordingly great. As the cuticle becomes thicker, the transpiration decreases, the minimum occurring when cuticular transpiration is still small and the stomatal transpiration has not yet become large.

Burgerstein (*28, p. 59*) confirmed these results with the leaves of *Aesculus hippocastanum*. Three leaves of different ages were cut from the same shoot, placed with the petioles in a closed beaker, and weighed after 2 and 24 hours. The youngest leaf lost 35.2 percent of its original weight, the middle-aged leaf 37.4 percent, and the oldest leaf 45.5 percent. But when calculated on the basis of 100 cm^2 of surface, the losses were 31.7, 21.5, and 34.5 g, respectively.

Extensive researches with various woody plants were carried out by Seeliger (*188*), who used a method similar to that described above. In every case maximum transpiration was found in leaves that had not reached half their final size. After reaching this maximum, the transpiration decreased and reached a constant value (in *Acer psuedoplatanus* L. and *Prunus cerasus* L.) or it continued to a minimum which was not reached until the leaf was almost mature (*Populus deltoides* Marsh.). This was followed in completely grown leaves by an increase in transpiration which continued for a long time with slight fluctuations.

Bergen (*14*) found, however, that branches of the evergreen-hardwood vegetation of the Mediterranean with leaves 15 to 18 months old gave off more water per unit area or per unit of weight than leaves 3 to 6 months old. Thus, old *Quercus ilex* L. leaves transpired three and one-half times as much as younger leaves. Von Guttenberg (*77*) found similar results, although his ratios differed in some cases.

In order to explain this greater transpiration in older leaves Bergen covered the underside of old and young leaves with cocoa butter. Since the ratio of the transpiration "without butter" to that "with butter" was greater in young leaves than in old ones, he concluded

that the reason for the greater transpiration in the older leaves lay in their greater cuticular transpiration.

Von Guttenberg repeated the experiment of Bergen and got contrary results: The ratio of the transpiration "without butter" to that "with" was greater in old leaves than in young ones. Since in July the young epidermis is more permeable than the old, the reasons for the greater transpiration of the old leaves must rest entirely on their stomatal behavior. The reason Von Guttenberg's results differed from those of Bergen probably lies in the fact that Bergen carried on his experiments in late summer and thus with older leaves; it seems that leaves which persist more than 1 year become more permeable the second summer. With leaves lasting only one season, however, the results of various workers agree in general that transpiration from younger leaves is greater than from older ones. The cuticular transpiration of a very young leaf is so large that the total transpiration at this time is at a maximum. If these youngest leaves are covered with hairs or are protected otherwise against transpiration, the maximum may be postponed to a later period. As the cuticle thickens in the growing leaf, the transpiration rapidly diminishes, but at this time the stomata commence to form so that transpiration again increases.

However this may be, most workers in this field are agreed, as witness the recent results of Schmucker (*186*) for linden, that the cuticular transpiration of freshly unfolded leaves is high. Schmucker also reports that the transpiration of young conifer shoots is high in comparison with that of more mature branches, when measured in terms of absolute water loss, but that in terms of green weight it is comparatively low.

In this connection it may also be mentioned that the number of stomata per given area is greater in young leaves than in old leaves, as shown in the following tabulation by Seybold (*189*):

	Number of stomata per mm² on under side of leaf
Ficus elastica Roxbg.:	
Young	260
Old	145
Olea europaea L.:	
Young	1,072
Old	625
Acacia decipiens R. Br.:	
Young	153
Old	96
Pinus cedrus [probably *P. cembra* L.]:	
Young	96
Old	32

Red leaves of *Cornus sanguinea* L. containing anthocyan transpire more slowly than green leaves, according to Linsbauer (*137*). Similar results were found by Stahl (*203*) in yellow and red autumn leaves. Since the stomata of such leaves are generally closed, this may explain the decreased transpiration. Even in *Salix*, which ordinarily does not close its stomata when wilting, the stomata were found partly closed in the autumn leaves. Molisch (*156*) obtained the same results, but it is doubtful whether this closing of the stomata can explain the decreased transpiration in the red *Cornus* leaves. Here the explanation is rather to be sought in the higher osmotic concentration of the sap of cells containing anthocyan. The higher the osmotic pressure the less the transpiration, other factors being equal.

Relation of Surface to Volume

Huber (*105*) attaches great importance to the ratio between the surface of the leaf (as measured in square centimeters) and the volume (in cubic centimeters, as measured by multiplying the thickness of the leaf by the surface). Since the number of cells transpiring into the internal air spaces of the leaf will vary with the volume, while the number of stomata varies with the surface, it is easy to see that the relation between the surface and the volume is important, especially in succulent leaves. Huber found that the figure 200 represents about the maximum size of this ratio and also that, from an ecological point of view, trees growing in drier sites tend to a smaller development of the transpiring surface, although this effect of humidity may be masked by the effects of light or other site factors. Thus *Fagus sylvatica* leaves (shade) show a ratio of 153, *Quercus pedunculata* Ehrh. leaves (sun) 84, and *Q. ilex* 70; the thickness of these leaves is 0.13, 0.21, and 0.28 mm, respectively. Conifers show an exceptionally small ratio (30 to 50).

Specific Variations

As has been indicated above, there are great specific variations in the transpiration of leaves, dependent in part, of course, on the factors already mentioned. Thus, Haas and Halma (*78*) found a considerable variation in the transpiration of various *Citrus* species. Both rooted cuttings and detached leaves of Eureka lemons transpired more than Marsh grapefruit, which in turn transpired more than Valencia oranges. The relative rates of water loss per unit surface during August and September were about 4.5:3.25:3. Such figures, however, have little value so far as specific differences are concerned unless we know all of the other factors involved; but they are valuable from the point of view of relative water loss and the resultant water requirement, in connection with which subject they will be discussed further. In fact the term "specific variations" is, for the most part, a subterfuge to hide ignorance as to the real causes.

Conifers and Broad-leaved Trees

Broadly speaking, as shown by some of the previous workers mentioned, there is a distinct difference between the transpiration rates of conifers and broad-leaved trees. During the active growing season the broad-leaved trees transpire much more rapidly than do the conifers, but the latter transpire over a much longer period of time; so that in considering total water utilization one must take into account not only the rate of transpiration but also the duration.

Weaver and Mogensen (*229*) studied 2- to 4-year-old seedlings (in pots) of *Pinus banksiana*, *P. ponderosa*, *P. murrayana* Balf., *Abies grandis* Lind., *Picea engelmanni*, *Pseudotsuga taxifolia*, *Acer saccharinum* L., *Quercus macrocarpa*, and *Ulmus americana* L. In the middle of the summer the broad-leaved trees transpired per unit area about 2.8 times as much as the conifers, but in the fall the conifers lost about as much per unit area as the broad-leaved trees or even more. In the winter the conifers transpired only 0.5 to 2 percent as fast as in the autumn, even with sufficient soil moisture—a transpiration rate only slightly greater than that of defoliated deciduous trees.

The difference between the transpiration of conifers and hardwoods has been observed for many years. One of the earliest workers in this field was Lawes (*133*), who, at intervals over an entire year,

weighed potted seedlings, ranging in size from 2 to 25 ounces, of various conifers and hardwoods, recording at the same time the daily temperature and the humidity. Since the evaporation rates were not compared with the leaf surface or weight, these results have little quantitative value, but even a casual glance at his numerous tables shows the increased evaporation of the hardwood species as compared with conifers.[3]

According to Hartig (*90*) the transpiration per unit area in the alder, beech, birch, oak, and aspen is to that of pine, larch, and spruce on the average as 2.5 is to 1. Vogel (*221*) found the transpiration ratio of beech in small trees taken from the forest and planted in a flask containing some of the original forest soil was to that of spruce as 5 is to 4, measuring the evaporation by loss in weight.

Von Höhnel (*100*), in order to study this question, cultivated in pots small (5- to 6-year-old) trees of *Acer*, *Betula*, *Fagus*, *Quercus*, *Tilia*, *Ulmus*, *Abies pectinata* DC., *Picea excelsa* Link, *Pinus laricio* Poir., and *P. sylvestris* L. Each pot was placed in a galvanized cylinder and the soil was well protected from the air; 36 plants were put under a shed and 30 in the open. The plants were weighed daily, morning and evening, from May 27 to December 21, and the temperature and humidity were recorded. In general the broad-leaved trees transpired 8 to 10 times as much during the summer months as the conifers. The next summer the experiment was repeated with about 100 trees from April 1 to October 15 in the open and from then on to the first of the following March indoors. Because of the higher temperature and the decreased precipitation, the broad-leaved trees this time transpired only about six times as much as the conifers. From these two sets of experiments, one may conclude, therefore, that under favorable conditions seedling broad-leaved trees will transpire about eight times as much as conifers.

Morosov (*159, p. 113*) calls attention, however, to the errors in the work of Von Höhnel and points out that 8 to 12 pounds of earth was much too little for trees 5 to 7 years old, and that the hermetical seal was bound to result in some degree of root suffocation, to which he attributes the high mortality of the seedlings. Possibly, also, the internal temperature of the zinc pots was too high. Furthermore, Von Höhnel calculated the amount of transpiration as based only on the weight of the leaves, without taking into account the increment of the stem and roots.

Kusano (*131*) compared the winter transpiration of conifers (*Chamaecyparis*, *Cryptomeria*, *Torreya*, and *Pinus thunbergii* Parl.) in Japan with that of broad-leaved evergreens (*Quercus glauca* Thunb., *Eriobotrya*, etc.). The average transpiration loss in percentage of fresh weight and of dry substance is shown in table 6.

TABLE 6.—*Average transpiration loss in winter of conifers and broad-leaved trees*

Tree type	Jan. 17–24		Mar. 21–24	
	Percentage of fresh weight	Percentage of dry substance	Percentage of fresh weight	Percentage of dry substance
Conifers	8.18	19.72	39.16	93.90
Broad-leaved	16.58	37.74	64.65	150.18
Ratio	1:2.02	1:1.9	1:1.65	1:1.6

[3] This paper also has an added historical value, since the author cites some of the earliest experiments in the field of transpiration, namely, those of Woodward in 1691 and of Hales in 1727.

The broad-leaved trees are thus seen to transpire twice as much as the conifers in January and 1.6 times as much in March.

ENVIRONMENTAL FACTORS

Light—Sun and Shade Leaves

Many studies have been made on the relation of light to transpiration, and for some years these studies seemed quite contradictory; but within the last few years the contradictions have been ironed out and considerable order is being developed from the previous chaos. Light, first of all, tends to produce a thickening of the leaves (i. e., a xeromorphic condition), especially in regions where water is lacking, this interrelation between the light and the water supply being one of the principal reasons for the contradictions in the literature.

Some authors found that light caused a checking of transpiration, while others reported an increase, and not until it was found that the result obtained depended largely upon the amount of available water was it possible to reconcile conflicting results. Measurements of transpiration in sun and shade leaves may also differ, depending upon whether the transpiration is related to the dry weight of a leaf or to the leaf area. If a beech leaf grown in the shade seems to evaporate more per unit of dry weight than one grown in the sun, this may be due to the more delicate nature of the former as compared with the tougher character of the latter. Hence it is quite possible for the transpiration per unit of weight of sun leaves to be less and yet for the total amount of water transpired by them to be more, as pointed out by Büsgen and Münch (*33, p. 228*). Light thus affects transpiration either (1) indirectly, by influencing the structure of the leaves, or (2) directly, through its effect upon the water loss itself.

The effect of light in changing the structure of the leaf has been reported by many authors. Grosglik (*76*) showed that the mesophyll of *Eucalyptus globulus* Labill. was thicker, especially the palisade tissue, in the presence of strong light. Géneau (*68*) likewise showed that the palisade layer of shade leaves in *Salix rosmarinifolia* Hort. was 0.06 mm thick while that of the sun leaves was 0.15 mm. In *Quercus pedunculata*, the corresponding figures were about 0.04 mm and 0.09 mm. Stahl (*202*) showed that the sun leaves of *Fagus* were 3 times as thick as the shade leaves, while Géneau reported that the sun leaves of *Taxus baccata* L. were about 1.4 times as thick as the shade leaves. In *Q. pedunculata* the sun leaves were 1.7 times as thick as the shade leaves, while the sun leaves of *Fagus sylvatica* were twice as thick as the shade leaves. Stahl also showed that the cells of the mesophyll were more compact in sun leaves so that the intercellular space was considerably smaller. In *Sambucus* he calculated that the volume of the intercellular space was 16 percent of the leaf volume in sun leaves and 26 percent in the shade leaves; in *Fagus* these figures were 19 and 29 percent, respectively.

Nordhausen (*163*) thought that these differences were not the direct result of light but were predetermined by the conditions (light, humidity, etc.) under which the buds formed the previous year. Maximov (*148, p. 347*), however, points out that these structures in the developed leaves are not indirect aftereffects produced in the leaf structure by the environmental conditions of the previous year but are direct effects of the stem structure, which are in turn determined by the environmental conditions. The water supplied to the

developing leaves is determined by the wood structure of the stem axis formed the preceding year, and if conditions were unfavorable for its development, the decreased conduction facilities result in a more xeromorphic leaf structure.

Brenner (*21*) thought that the sun leaves of oak were generally smaller than the shade leaves, but Burgerstein (*28, p. 55*) states that this was not the case in many species, and that in *Q. pedunculata* as well as in *Carpinus*, *Fagus*, *Acer*, etc., the sun leaves were larger than the shade leaves. However, Brenner's findings that the sun leaves generally had thicker outer epidermis walls than the shade leaves and that there were more layers of palisade cells agree with results of other workers.

Because of this thickening, it was held that sun leaves should transpire less than shade leaves and this was the opinion of Von Höhnel, who found that the mean transpiration per 100 g air-dry weight in a broad-leaved tree from April 1 to October 31, 1879, was: Shade specimen, 94.35 kg; half shade, 88.78 kg; sun 62.68 kg. When conifers and hardwoods were compared, he found that the hardwoods transpired more in the shade than in the sun, while the reverse was true of conifers, as shown in table 7.

TABLE 7.—*Relative amounts of water transpired by conifers and hardwoods in the sun and in the shade*

Species	Sun	Shade	Species	Sun	Shade
	Kg	*Kg*		*Kg*	*Kg*
Beech	76.2	107.8	Fir	13.9	4.8
Hornbeam	86.3	98.9	Pine	19.1	5.0

As has been mentioned above, however, Von Höhnel's method of procedure is open to considerable objection and, if there had been an abundance of water and plenty of air, doubtless the sun leaves of the hardwoods would have transpired more than those in the shade, the reason for the decrease being that water was the limiting factor.

Table 8 shows the difference between larch plants in sunlight and in half shade from April to October. Here also it will be noted that most of the time these plants transpired more in the shade than in the sun, but here, again, water was probably a limiting factor in the sun.

TABLE 8.—*Transpiration per 100 g of air-dry weight of leaves of larch plants in sunlight and in half shade, April to October*

Month	Sunlight	Half shade	Month	Sunlight	Half shade
	Grams	*Grams*		*Grams*	*Grams*
April	2.82	2.97	August	21.80	33.11
May	7.16	6.00	September	44.66	16.90
June	10.82	14.42	October	21.96	6.56
July	16.10	24.46			

The view that shade leaves transpired more than sun leaves was held also by the other workers in this period until the careful experiments of Géneau (*68*), who showed that the intensity of transpiration of sun leaves was not less but even considerably greater than that of

shade leaves. Using six different methods, he studied very carefully the relative transpiration of sun and shade leaves of the same species placed in the same environment. The method which he considered the best was that of weighing rooted plants grown in watertight vessels from which soil evaporation was prevented. The results of all six methods, however, were consistent and in every case the leaves developed in the sun showed a higher transpiration intensity than leaves developed in the shade, whether in light or in darkness. Sun and shade leaves of the oak transpired, during 1 hour, 170 and 110 mg per square decimeter; beech 240 and 110; and yew, 110 and 40, respectively. At the time, these results were viewed with a great deal of skepticism, since it was thought that plants in the sun should have methods of checking transpiration.

Géneau's results have been confirmed by many workers, including Bergen (*13*), who used evergreen broad-leaved species. Twigs were cut, placed with the cut end in water, and weighed at regular intervals. When the sun leaves were in the sun and the shade leaves in the shade, the former transpired about three to six times as much as the shade leaves; but when both were in the sun or both in the shade, the sun leaves transpired only one to two times as much as the shade leaves per unit of surface. These leaves, on the whole, evaporated only about 25 percent less than *Ulmus campestris*, a distinctly thin-leaved species.

Huber (*109*) reported that sun leaves of oak always transpire as much as shade leaves and generally more. Since their area is smaller they really transpire more per square centimeter. Kamp (*119*) found that the loss of water from sun leaves of various species was much more than that from shade leaves of the same species, and that the dorsal surface of the sun leaves lost much more than that of the shade leaves. Hesselman (*95*) also has shown that in sun leaves of beech with many palisade cells there was more water transpired in proportion to the leaf surface than from shade leaves of the same locality.

Hanson (*83*), working with *Ulmus*, *Acer*, and *Fraxinus* in Nebraska, concluded that five-sixths of the transpiration from the tree was from the peripheral branches and only one-sixth from equal areas on shaded branches. The evaporation at the south edge of the crowns was one-half to two and one-third times that within the crown. The leaves from the south edge also show a much more xerophytic structure (thicker, more palisade tissue, etc.) than those inside the crown. In *Fraxinus pennsylvanica* Marsh. the leaves at the south margin lost three to six times as much water per unit area as those within the crown, while in *Ulmus americana* the marginal leaves transpired 12 times as much per unit area as the interior leaves.

Cribbs (*40*) in his fairly comprehensive studies on transpiration in *Tilia* found a distinct correlation between transpiration and light intensity when other factors were about equal. In ecological studies, however, it is impossible to isolate individual, experimental factors; in such studies one is forced, by the nature of things, to study the effect of the site as a unit.

Some experimental work in this general direction was carried on by Burns and Hooper (*29*, *30*), who planted seedlings of *Pinus strobus* in the open in three different beds, one of which was left exposed to the sun while the other two were placed in half shade and full shade, respectively. Transpiration (determined by weighing) of the un-

shaded plants was 5 to 21 times that of the plants in full shade and 2 to 3 times that of the plants in half shade, which transpired 3 to 8 times as much as those in full shade. The evaporating power of the air, as measured with both black and white atmometers, showed that the plants followed the black atmometers more closely than the white.

Weaver and Thiel (*230*) placed in various environments potted seedlings of *Acer saccharinum* that had been grown in the sun and shade. In the sun, the shade plants lost 35 percent as much water as the sun forms in a given unit of time. Similarly a cut branch from the center of an elm tree lost 11 percent as much as one from the edge.

Bartholomew (*10*) reported that *Citrus* plants subjected to total darkness for 2 hours in the middle of the day lost only one-third the amount transpired in the same period before or after in indirect sunlight. Among the most recent results in this field are those of Biswell (*16*), who measured the water loss in grams per square inch of leaf area, in full insolation and in half shade, of five species of trees in Nebraska. The mean annual precipitation during the last 20 years in this section was 37 inches, which is generally well distributed throughout the growing season. The wind measurements and evaporation losses from atmometers were recorded. Table 9 shows that in every case transpiration in half shade was less than in full sunlight.

TABLE 9.—*Average water loss per square inch of leaf area of leaves of 5 hardwood species, in full sunlight and in half shade, in 2 weekly periods*

Species	Water loss					
	July 4–11		July 12–19		Average	
	Sun	Half shade	Sun	Half shade	Sun	Half shade
	Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
Boxelder	6.66	5.24	5.03	2.93	5.85	4.08
Sycamore	8.04	6.82	7.95	6.45	8.00	6.64
Buckeye	7.24	6.62	7.25	5.25	7.25	5.99
Red oak	8.38	4.87	6.28	4.16	7.33	4.52
Hard maple	11.00	4.46	11.08	4.43	11.04	4.45

While these results all show that transpiration is greater in the light than in the shade, it is surprising how variable results may be. Thus, Stahl (*203*) found that a potted *Ficus* plant in Europe transpired 102 times faster in the sun than when on the back wall of a room facing the north, while Haberlandt (*80*) found that a *Ficus* leaf in Java transpired in a sunny forenoon only 12 times as much as in the evening, per unit of time. It is, of course, very difficult to compare results in two different localities unless one has accurate measurements of all the other factors involved.

Some work has been done (though not much on trees) on the effects of different colored light on transpiration. These experiments agree in general in showing that the rays which influence photosynthesis most, i. e., the ones that are most absorbed by the leaf, increase transpiration most; these are the rays in the orange-red and blue regions.

In summing up the work on light, one may say that, everything else being equal, plants transpire more in light than in its absence and that transpiration increases with the intensity of light, provided there is an abundant supply of moisture. When water is lacking or if the site is notably dry, the transpiration of the shade leaves may exceed that of the more xeromorphic sun leaves. Also, as pointed out by Wiesner (*238*), a plant taken from the darkness into the light shows at the beginning stronger transpiration than it does later on, when it finally reaches a stationary value. The same thing happens when a plant is brought from the light into the darkness; the change causes an original increase, which later decreases to a constant value. In this latter case the stationary value is arrived at earlier than when the plant is taken from the darkness into the light.

The explanation of these phenomena is probably not simple but depends on various factors. Wiesner has shown that both heat and light rays increase the transpiration, and he explains the effect of these rays by assuming that they increase the permeability of the plasma membranes of the transpiring cells; this increase in permeability naturally permits an easier escape of the included water. The effect of light is probably associated with very complicated reactions, accompanied by the transformation of the light rays into heat, but for a discussion of the physics involved, the reader is again referred to Seybold (*189*). One must not confuse the effect of light on permeability, however, with that of water deficiency, which tends to decrease the permeability of sun leaves, as pointed out by Huber (*109*).

Other less abstruse factors, however, are present. A part of the increased transpiration in sun leaves can be explained by the greater number of stomata (20 to 60 percent greater per unit surface) they contain and by the difference in their chlorophyll content. Hesselmann (*95*) was among the first to call attention to the increased number of stomata in sun leaves in general, and his results have been confirmed by other workers interested especially in trees. Table 10, giving data from the work of Schramm (*181*), shows the difference in the number of stomata per square millimeter in sun and shade leaves of various woody species.

TABLE 10.—*Number of stomata per square millimeter in shade and sun leaves of various tree species*

Species	Stomata per square millimeter in—		Species	Stomata per square millimeter in—	
	Shade leaves	Sun leaves		Shade leaves	Sun leaves
	Number	*Number*		*Number*	*Number*
Fagus sylvatica L.	113	416	*Acer pseudoplatanus* L.	215	860
Quercus sessiliflora Salisb.	468	810	*Fraxinus excelsior* L.	478	1,265
Ulmus campestris L.	450	800	*Tilia platyphyllos* Scop.	450	759
Alnus glutinosa Gaert.	425	608	*Sambucus nigra* L.	70	165
Carpinus betulus L.	170	365	*Cornus mas* L.	162	364

In consequence of their greater number of stomata and the fact that stomatal transpiration is much greater than cuticular, sun leaves transpire more than shade leaves. Shade leaves also have less need for cuticular protection against evaporation, and since they are

constructed to favor transpiration, they can transpire at the necessary rate even in the moist, calm interior of the crowns.

Another factor which helps to explain the increased transpiration in sun leaves is their increased number of veins, as shown in table 11 (also from the work of Schramm). This greater nervature permits an added flow of water to the leaf; otherwise the increased number of stomata could probably not be supplied with sufficient water.

TABLE 11.—*Length of veins per square millimeter of shade and sun leaves of various tree species*

Species	Shade leaves	Sun leaves	Species	Shade leaves	Sun leaves
	Mm	*Mm*		*Mm*	*Mm*
Fagus sylvatica	8.8	12.2	*Acer pseudoplatanus*	5.6	7.8
Quercus sessiliflora	9.9	14.3	*Fraxinus excelsior*	9.3	11.8
Ulmus campestris	10.5	17.2	*Tilia platyphyllos*	8.4	12.1
Alnus glutinosa	3.6	8.1	*Sambucus nigra*	3.6	6.1
Carpinus betulus	6.9	9.8	*Cornus mas*	7.9	11.4

These differences in structure probably explain the results of Huber (*110*), who found that, when left to dry, the shade leaves of *Quercus pedunculata* checked transpiration more rapidly than did the sun leaves, especially during the first hour; but it took the sun leaves 2 days longer to become air-dry. The shade leaves, in other words, close their stomata more rapidly in case of water deficit, but the greater cuticular protection along with other physiological factors determines the better resistance of the sun leaves to prolonged drought. Kisselew (*122*), however, found that while the shade leaves of *Syringa* and *Caragana* wilted more rapidly than the sun leaves, this was not the case with *Tilia* and *Acer*.

In connection with the increase of the nervature in sun leaves, it is interesting to note that this increase is very marked with increasing height above ground in sun plants but is very slight in the case of shade individuals, with the result that translocation of nutrients as well as absorption of water is impeded in shade plants. This accounts for the fact (which Burgerstein regarded as paradoxical) that the thin, tender leaves of shade plants transpire less than the better protected leaves of sun plants. As Maximov (*148, p. 353*) has pointed out, it is the deficient water supply rather than the intense transpiration which explains the ease with which shade plants wilt; and it is this insufficient water supply which Zalensky (*248*) has called "internal physiological dryness."

Huber (*105*), as stated above, has been much interested in the water supply of sun and shade plants and has pointed out that for the former the ability to transfer water rapidly to the evaporating cells is of great importance. He thus calculated the conductivity of xylem in sun and shade branches of oak, comparing the conductivity with the transpiration loss, and found that a sun branch transpired 75.7 mg per square decimeter per hour, while the shade branch transpired 45.9 mg, or only about two-thirds as much. On the other hand, the cross section of the conducting tissues per square decimeter of leaf surface in the shade shoot was 0.20 mm^2 and in the sun shoot 0.42 mm^2; that is, the area of the conducting tissue in the former is only one-half what it is in the latter. But since the transpiration of the shade leaf is two-thirds that of the sun leaf, the rate of flow in the vessels must

be greater, even though the total transpiration is less, than in the sun shoot. It is not surprising, therefore, to find that when shade leaves are placed in the sun they wilt more readily than the sun leaves, in spite of a lower absolute water loss.

The transpiration in turn influences the amount of the conducting tissue, especially the number and width of the wood elements in the vascular bundles, as pointed out by Kohl (*127*) and later by other authors. Winkler (*242, pp. 65–79*) showed that plants which transpire heavily build vessels with wide lumina, and vice versa, and came to the conclusion that between the amount of transpiration and the mass of conducting tissue there was a decided correlation. Also, plants which have to absorb relatively large amounts of water in a comparatively short time have well-developed vascular tissues, as pointed out by Cannon (*34*) in the desert plants of Arizona. *Covillea*, *Parkinsonia*, *Prosopis*, etc., which take in most of their water during the one or two rainy periods of the year, have a larger number of vessels per unit cross section of stem than those which obtain their water more uniformly throughout the growing season. Not only are the vessels greater in number but the individual conducting elements are larger, according to Groom (*75*), who reports that the American species of pine with narrow tracheids (0.024 to 0.039 mm) generally live in drier habitats than those with wider tracheids (up to 0.05 mm). The width of the wood elements in the various species varies with the moistness of the habitat, although it should be noted, as pointed out by Büsgen and Münch (*33, p. 182*), that there are many exceptions to this general rule, and the determining climatic and edaphic conditions are frequently difficult to analyze exactly. The change from spring to fall wood is associated also with the water supply and supports the above conclusions. As to experimental work on this subject, we have the results of Wieler (*235*), who found that small trees of *Robinia* and *Quercus sessiliflora* Salisb. in nutrient solutions, where there was an abundance of water and a moist atmosphere, produced wood with abnormally wide conducting elements.

This relation between the conducting system and the ability of trees to replace water losses has been studied also by Stefanoff and Stoickoff (*208*), who reported that in conifers water is conducted to the leaves about as rapidly as it is lost, permitting only slight water deficits. The same is true of *Alnus glutinosa* Gaert., *Castanea vesca* Gaert., *Acer dasycarpum* Ehrh., *A. platanoides*, and *Carpinus betulus*. The evergreen broad-leaved trees, however, such as *Buxus* and *Prunus laurocerasus* L., and such trees as *Fraxinus oxycarpa* Willd., *F. excelsior*, *Morus alba* L., *Gleditsia triacanthos*, *Robinia pseudoacacia* L., *Juglans regia* L., and *Acer pseudoplatanus*, show heavy water deficits and cannot conduct water rapidly enough to replace transpiration losses even when an abundant supply is available.

The characteristic structures of sun leaves are consequently thought by many workers to be produced by drought rather than by light. To test this hypothesis experimentally Söding (*197*) studied the effect of physiological drought on small potted trees of *Tilia cordata* Mill., *Fraxinus excelsior*, and *Acer platanoides* by adding NaCl to the soil. The trees thus treated had smaller leaves and shorter shoots than the controls and showed all the characteristics of sun leaves and shoots, leading to the conclusion that such modifications are caused by water deficits in the tissues at the time of shoot formation.

Temperature

Temperature is another important factor influencing transpiration. Since temperature affects the diffusion of the water molecules from the cell as well as the general life processes of the plant, it is not surprising to learn that an increase in temperature is generally associated with an increase in transpiration. Wiesner (*237*) found that a leafy twig of *Celtis australis* L. in diffuse light gave off 0.22 cc of water at an average temperature of 4.3° C.; at 10° C., 1.2 cc; at 13° C., 1.8 cc; and at 16° C., 3.0 cc.

Roeser (*177*) studied the transpiration of various conifer seedlings in temperatures somewhat above the average. The purpose of the tests was not to get a measure of the maximum transpiration rate but to study the increase in transpiration rate produced by gradually increasing the heat to which the seedlings were exposed. Seedlings of western yellow pine, lodgepole pine, Douglas fir, and Englemann spruce were placed in narrow-mouthed bottles containing about 150 cc of water, with the roots entirely submerged. Readings at six different temperatures were obtained with a mercury thermometer whose bulb was placed at the level of the leaves. In all the tests the seedlings were illuminated by a 60-watt lamp, so that the light factor was constant. Results are given in table 12.

Table 12.—*Losses of water per minute by conifer seedlings at average and moderately high temperatures*

Temperature (° F.)	Ponderosa pine		Lodgepole pine		Douglas fir		Engelmann spruce	
	Loss per minute per gram of dry weight	Relative increase [1]	Loss per minute per gram of dry weight	Relative increase [1]	Loss per minute per gram of dry weight	Relative increase [1]	Loss per minute per gram of dry weight	Relative increase [1]
	Milligrams		*Milligrams*		*Milligrams*		*Milligrams*	
61.2	4.7	1.00	7.0	1.00	2.1	1.00	2.3	1.00
70.8	8.6	1.83	14.6	2.09	7.4	3.52	11.7	5.08
85.0	9.6	2.04	27.0	3.76	10.0	4.76	15.6	6.78
103.1	16.5	3.51	35.0	5.00	17.2	8.19	23.2	10.08
116.2	23.6	5.02	47.5	6.79	27.8	13.24	43.6	18.96
124.1	62.4	13.28	86.6	12.37	38.4	18.37	65.0	28.26

[1] Transpiration at 61.2° F. is considered as unity in giving relative increases at the higher temperatures.

It will be noted that lodgepole pine transpired much more than the other species. At the higher temperatures this was followed by spruce, Douglas fir, and ponderosa pine, the last two being very near each other. At the lowest temperature the ponderosa pine ranked second. Roeser interprets these data as showing that both Engelmann spruce and Douglas fir are apparently more capable of increasing their transpiration rate under severe conditions of heat than are the pines. He also noted that the amount and rate of transpiration dropped off as the seedlings grew older, the change being least rapid and most uniform in the ponderosa pine, which seems to be more consistent in its normal transpiration through the first year than any of the other three species. It thus seems possible to relate to some extent the transpiration ability of these seedlings to their natural site conditions.

Also, as a general rule, the transpiration rate decreased at any given temperature as the period of exposure increased for all ages up to 1

year, as shown in table 13, leading to the conclusion that seedling size determines the capacity of each species to prolong its transpiration.

TABLE 13.—*Effect of age on transpiration of conifer seedlings at room temperatures (69° to 77° F.) for about 16 hours*

Age of seedlings [1]	Ponderosa pine		Lodgepole pine		Douglas fir		Engelmann spruce	
	Average weight	Water transpired per gram of dry weight	Average weight	Water transpired per gram of dry weight	Average weight	Water transpired per gram of dry weight	Average weight	Water transpired per gram of dry weight
	Milligrams	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*	*Milligrams*
68 days	38	8.56	5.5	41.43	8	26.17	4	47.60
122 days	61	4.00	9	18.10	24	6.30	7	24.30
1 year	80	2.76	29	3.75	34	1.71	14	3.26

[1] Douglas fir approximately 26 days younger.

This dependency of transpiration upon temperature results naturally in daily and seasonal cycles. In the daily cycle especially, however, it is very difficult to separate the heat effect from that of light, since the two parallel each other very closely. Dole (*52*) found that *Pinus strobus* seedlings 6 to 8 years old showed a regular diurnal curve of transpiration. Beginning with about 15 to 20 g of water loss per plant per hour at 8 a. m., the transpiration rose to a maximum of over 30 g at about 3 p. m. and then decreased gradually until 8 p. m. to about 4 g. From then until 11 p. m. the transpiration fell off more slowly to about 2 g per plant per hour, remaining at this level until 4 a. m., when it again rose gradually through 8 a. m. to the 3 p. m. level. At the time of greatest transpiration the humidity was the lowest. He furthermore showed that with 3-year-old plants the absolute losses could not be correlated either with relative humidity, with temperature, or with their combined effect, as expressed in terms of vapor pressure. He interpreted his results to indicate that the temperature, in addition to its effect upon humidity, influenced the diffusion. This view is in accordance, as has been pointed out above, with the known physical effects of increased temperature.

Cribbs (*40*), in his series of studies on *Tilia*, found that when the soil moisture was plentiful the daily transpiration curve was very much like that reported by Dole, but that the time of maximum transpiration varied with the other factors which influence transpiration, namely, light intensity, relative humidity, soil moisture, and soil temperature. In exposed stations on sand the maximum rate was at 10 a. m., owing to a saturation deficit. A second (lower) rise then occurred in the afternoon. The depression of the transpiration rate, however, was due not to a lower soil-moisture content but to the inability of the tissues to conduct the water fast enough. In these studies, which will be referred to later, the rate of transpiration (transpiring power) was measured by the cobalt chloride paper method.

Blaydes (*17*), however, found that the time of maximum transpiration came much earlier in the day than the time of maximum evaporative power of the air. Evaporation studies with 148 species of plants in the deciduous forests of Indiana and Ohio, using the cobalt chloride paper method, showed that 93 percent of the plants reached their

maximum evaporation rate before noon, 89 percent before 11 a. m., and 52 percent before 10 a. m., the greatest number of maxima occurring about 9 a. m., whether the habitats were wet or dry.

The seasonal temperature cycle, while also affected somewhat by light, is easier to detect than the daily cycle, because the seasonal light variations are not so great as the daily ones, while the seasonal temperature variations are much greater. Clark (*36*) measured the transpiration rate from May 2 to October 17 of cut twigs of *Fagus grandifolia* Ehrh. and *Quercus alba* L. At various intervals twigs were removed from the trees to the laboratory and their daily losses in percentage of dry weight were recorded. Between 8 a. m. and 5 p. m. *Fagus* lost about 1.21 percent of the dry weight per hour, while *Quercus* transpired only 0.43 percent in the same period. Transpiration was highest in the spring and decreased fairly regularly until the fall, reaching a minimum at the time of leaf fall. The water content of the leaves, however, reached a minimum 1 to 2 months before leaf fall, leading Clark to conclude that there was no connection between the leaf water content and the transpiration, temperature, or relative humidity.

Weaver and Mogensen (*229*) reported similar decreases in transpiration in the late summer with *Ulmus*, *Acer*, and *Quercus*, and found that at this time of year in Nebraska the transpiration rate per unit area was no greater from broad-leaved trees (2 to 4 years old in pots) than from conifers. Their figures are as follows:

	Grams
Loss per square decimeter, July 20 to Aug. 15:	
Pinus ponderosa	2. 24
Pseudotsuga taxifolia	1. 95
Picea engelmanni	2. 24
Acer glabrum	4. 33
Acer saccharinum	5. 36
For the last week of September and the first week of October:	
Acer saccharinum, 9 trees	2. 66
Ulmus americana, 9 trees	3. 56
Quercus macrocarpa, 7 trees	5. 18
Picea engelmanni, 3 trees	4. 18
Abies grandis, 5 trees	5. 17
Pinus ponderosa, 3 trees	4. 20
Pinus banksiana, 3 trees	4. 80

This decrease in transpiration at the end of the summer in broad-leaved trees is undoubtedly associated with the fall of the leaves. According to most observers, the leaves at this time contain a smaller percentage of water. Furthermore, the conducting tissues between the leaf and the stem are being disconnected preparatory to abscission, and also the stomata are tending to close. All three of these factors doubtless play a role in the decreased transpiration at this period.

Molisch (*154*), who considered this problem from a general point of view, determined that when leaves of woody plants are placed in a saturated atmosphere so that the transpiration is decidedly checked, most of the leaves fall off in a few days; likewise, leaves accustomed to a moderate degree of humidity, when placed in a dry atmosphere, fall as soon as the abscission layer is formed. Thus, the fall of leaves both in the autumn and during drought periods in the middle of the summer, common in the case of pines, is probably associated more with the humidity and soil moisture than with temperature; but this question will be discussed further in the section devoted to humidity.

The work of Montemartini (*158*) should be mentioned briefly. He noted that in poplar the leaves at the ends of branches, i. e., the younger ones, were the last to fall; while in the mulberry, the last leaves to drop off were those at the base of the twigs, i. e., the oldest. He explains this by the fact that transpiration in the poplar is chiefly stomatal and the young leaves consequently control water losses better. In the mulberry, on the other hand, the transpiration is chiefly cuticular, and the oldest leaves are the better protected, i. e., cutinized, and consequently are the last to fall.

WINTER TRANSPIRATION

In winter, conifers still transpire, although the transpiration rate is very much reduced. Hartig (*88*) found that a *Picea* plant 3 feet high lost one-fourth of a pound of water a day in a mild winter; but since neither the leaf area nor the weight of the plant is given, this paper is chiefly of historical value.

Burgerstein (*26*) measured the transpiration of 1-year-old twigs of *Taxus baccata* L. with a special view to determining whether transpiration continued at low temperatures. He found, as shown in the following tabulation, a gradual decrease in the transpiration rate as the temperature decreased, but even at —11° C. there was a slight water loss.

Temperature (° C.) and loss of fresh weight per hour:

	Percent
+17	1.5
+12	.9
+4	.6
−2	.3
−6	.1
−11	.02

Ivanov (*114*) compared the transpiration in winter of 60 species of trees and shrubs from the arboretum at Leningrad. One-year-old twigs were cut and the cut surface closed with wax. The transpiration rate was then determined by direct weighing and the loss in weight calculated on the basis of the surface exposed. He used larch as his standard and compared the others with it, employing the term "relative transpiration." This is unfortunate, since (as has been pointed out) "relative transpiration", as proposed by Livingston and as used in the literature, has a very different meaning. Considering *Larix* as 1, however, the following transpiration rates were found: *Abies sibirica* Ledeb., 0.3; *Pinus cembra* L., 0.9; *P. sylvestris*, 0.6; *Picea obovata* Ledeb., 0.8; *P. excelsa*, 1.5. The amount of daily loss of water in winter in the moist climate of Leningrad was thus seen to vary around 0.4 percent of the fresh weight of the needle-covered twigs. The transpiration in summer was about 300 to 400 times as great as that in winter. This figure does not compare unfavorably with that obtained by Weaver and Mogensen (*229*), who found that in winter in Nebraska the transpiration of conifers dropped from one fifty-fifth to one two hundred and fifty-first of the autumn rate.

Transpiration of conifers in winter in Japan was compared with that of broadleaved evergreens by Kusano (*131*), who found that the latter near Tokyo transpired an average of 16.58 g per square decimeter of surface during the period January 17 to 24, while the conifers transpired about half this amount per square decimeter (8.18 g). The

temperature during this period ranged from −5.9° to 10.5° C., with an average of 1.9°. The relative humidity was 39 to 74 percent.

Even deciduous trees, however, lose water in winter. Hartig (*89*), who was one of the earliest investigators in this field, placed tips of twigs of various trees in closed test tubes. After about 24 hours the test tubes were replaced with dry ones; the weight of the original tubes showed the increase brought about by the moisture condensed on the inside. On the basis of these rather primitive experiments, he ranged plants according to the rate of water loss of their twigs in the following order: *Alnus*, *Quercus*, *Robinia*, *Fagus*, *Juglans*, *Betula*, *Tilia*, *Acer*, *Fraxinus*, *Pyrus*, *Aesculus*, *Ulmus*, *Salix*.

Burger (*24*) in interpreting the work of Von Höhnel reported that hardwoods lost only 0.5 to 2.5 percent of their annual water loss in the winter, while conifers lost 8.5 to 12 percent of their annual transpiration at this season. Larch (deciduous) in this respect is similar to the hardwoods with a winter transpiration of 1.4 percent, while in beech and spruce the corresponding figures are 1.5 and 12 percent, respectively. Since these plants were in a closed though unheated room, it is to be supposed that these figures are somewhat below those under natural conditions.

Wiesner and Pacher (*241*) found that transpiration in 2- or 3-year-old twigs of *Aesculus* and *Quercus* continued at a noticeable rate even at −3.5° to −13° C., as indicated in table 14. They also studied the transpiration of *Aesculus* twigs 1 to 30 years old, removing the buds and sealing the cut places with wax. They found, among other results, that the amount of water given off varied inversely with the age, since the older twigs seemed to be better adapted for conserving moisture.

The following is a sample of their results:

Age of twigs (years) and loss of water in 10 days at 15° to 17° C.:

	Percent
1	11.53
2	10.80
3	9.46
4	6.11
5	5.00
10	4.39
15	3.47
30	1.83

Similar results were obtained by Ivanov (*114*) with 1- and 2-year-old shoots of *Aesculus glabra* and *Juglans cinerea* L. The relative rates of transpiration of the 1- and 2-year-old shoots in *Aesculus* were as 4.59 is to 2.46 and in *Juglans* as 6.53 is to 4.25.

TABLE 14.—*Water loss at temperatures below 0° C. of twigs of Aesculus and Quercus in 24 hours*

Species and age	Average temperature	Water loss in 24 hours on basis of original weight
	°C.	*Percent*
Aesculus, 2 years	−7.00	0.32
	−9.25	.20
Quercus, 3 years	−7.00	.23
	−9.25	.19

Similarly young *Taxus baccata* twigs (deprived of leaves when cut) lost water much more rapidly than older twigs, as shown by Wiesner and Pacher (*241*), who report the results shown in table 15.

TABLE 15.—*Water losses in first 6 days after cutting and removal of leaves from Taxus baccata twigs of different ages*

24-hour interval	Water loss (on fresh-weight basis) of—			24-hour interval	Water loss (on fresh-weight basis) of—		
	2-year-old twigs	3-year-old twigs	4-year-old twigs		2-year-old twigs	3-year-old twigs	4-year-old twigs
	Percent	*Percent*	*Percent*		*Percent*	*Percent*	*Percent*
First	28.5	16.4	8.5	Fourth	1.2	6.1	4.5
Second	15.1	11.7	7.2	Fifth	.4	2.8	3.7
Third	3.0	8.5	5.4	Sixth	.4	1.2	2.9

Kny (*125*) placed sections of winter branches of broad-leaved trees in a room at 15° C., noting the water losses. In *Fraxinus excelsior*, *Acer pseudoplatanus*, and *Ulmus scabra* Mill. the losses were considerably greater between the nodes than at the nodes where the buds are located, while in *Carpinus betulus* and *Aesculus hippocastanum* there was little difference in this respect between the stem sections. Buds of *Syringa*, *Fraxinus*, and *Aesculus* showed larger losses in weight when the leaf scars were plugged up. There is no doubt, therefore, that 1-year-old twigs can lose considerable amounts of water through transpiration during a dry winter.

A large part of the evaporation from the twigs is from the lenticels, which various researchers have shown serve for gaseous exchange on the young twigs in very much the same way that the stomata serve on the leaves. Haberlandt (*79*) thought that the lenticels were closed much of the time even in summer in many trees (e. g., *Tilia* and *Robinia*). These results, however, were not supported by the work of Klebahn (*123*), who concluded from the results of studies on over 70 different species that (1) lenticels are open both in summer and winter and that (2) in many cases their permeability is nearly as great in the winter as in the summer.

It is also interesting to note in this connection that the lenticels are much less permeable to air (and the contained moisture) when moist than when dry. As pointed out by Zahlbruckner (*247*), differences were especially noticeable in *Ailanthus altissima* Swingle, *Alnus glutinosa*, *Caragana frutescens* DC., and *Paulownia imperialis* Sieb. and Zucc.

The relative proportion of the transpiration from the twigs through the lenticels has been studied especially by Haberlandt and Klebahn. The cut ends of the twigs were closed with wax or lacquer and drops were placed over the lenticels. Similar twigs were prepared in which the same number of drops of wax were placed between the lenticels, and the relative water losses of the two twigs were then compared, differences being considered as due to the lenticels. Klebahn found that twigs of *Morus alba* in 3 days lost 46 percent of their original weight when the lenticels were closed and 80 percent when they were open. This loss of water from deciduous trees in winter may be considerable in the aggregate, and it is doubtful whether all foresters have

appreciated this sufficiently in calculating the annual losses of water from forests.

Thus, Ivanov found that 1-year-old twigs of deciduous trees in the vicinity of Leningrad lost more water per surface area in the winter than did the conifers, the figures for which have been given above. While *Larix* transpires 1 (the standard used by Ivanov), 1-year-old twigs of *Acer pseudoplatanus* transpired 1.6, of *Populus nigra* L. 1.1, and of *A. tataricum* L. 2.7.

Weaver and Mogensen (*229*) found also, it will be recalled, that in winter the transpiration of conifers in Nebraska was only slightly greater than that from defoliated deciduous trees; and Thren (*213*) has recently reported that during a short cold spell in Germany if the transpiration of *Pinus* was 1, that of *Picea* was 0.64 to 2.09, of *Fagus* 0.34 to 1.07, and of *Quercus* 0.52 to 1.36, indicating that winter transpiration in hardwoods is not far behind that in conifers.

The fact that winter buds also transpire has been noted. Wiegand (*234*) exposed buds of *Pinus laricio* and *Aesculus hippocastanum* for 3 days in the open at a temperature of −7° to −18° C. Some (a) remained continuously exposed to the cold, while others (b) were brought 10 times for a few moments during the period of observation into a warm laboratory. The percentage loss of the original water content as shown by weighing is as follows: *Pinus* (a) 3.4, (b) 5.0; *Aesculus* (a) 0.4, (b) 0.6. Buds in general transpire more in winter than branches, and it was upon this basis that Ivanov explained his results with long and short twigs; the fact that twigs with long internodes transpired relatively less than those with short internodes, he explained as due to the fact that the shorter ones had a higher proportion of buds. A sample of his results, giving relative transpiration (based on *Larix* as 1), is as follows: *Acer pseudoplatanus:* long internode twigs, 1.6, short internode twigs, 4.0; *Populus nigra:* 1.1 and 6.3; and *P. tremula* L.: 1.9 and 5.8, respectively.

Transpiration in 1-year-old twigs of trees in winter was found by Ivanov (*114*) to vary with the latitude and, according to him, species of southern origin transpired more than those of northern in the genera *Acer*, *Salix*, *Betula*, *Tilia*, and *Ulmus*. As a sample of his results is here recorded the *Acer* series:

	Transpiration rate (Larix=1)
Acer platanoides	1.45
A. pseudoplatanus	1.60
A. campestre L.	2.53
A. tataricum	2.68

On the basis of these findings, Ivanov concluded that in general the weak transpiration enabled the trees to spread farther northward, because as one proceeds northward, the amount of available water in the soil in winter becomes less and less. The northern distribution is thus connected with the physiological dryness of the site. In many cases the transpiration figures support the thesis of Ivanov; *Abies sibirica* and *Picea obovata*, for example, showed a transpiration rate of 0.3 to 0.8, and these species are among those found farthest north. One should be warned, however, against assuming that this is the only factor determining the northern distribution of species, as pointed out by Rubner (*178, p. 72*).

SOIL TEMPERATURE

In addition to air temperature, the temperature of the soil is an important factor in the transpiration of trees. Yendo and Yamashita (*244*) showed that in the mulberry the transpiration stream began in March as soon as the soil temperature had reached 5° C.; but Ikeda (*112*), working on the same problem, recorded 4° as the critical soil temperature for the flow of the transpiration stream in this species. Cribbs, also in the studies already referred to (*40*), concluded that the temperature of the soil was one of the most important factors in the transpiration of *Tilia*, since the transpiration curve ran very nearly parallel to that of soil temperature.

Humidity and Factors Influencing It

Of all the characteristics of the atmosphere which influence transpiration, by far the most important is the water-vapor content. The amount of water given off by plants or by any moist surface to the air will depend on the amount of water vapor already present in the air; and that transpiration varies inversely with the relative humidity is a fact so well known that it seems hardly necessary to call attention to it. Most of the numerous papers published on this subject deal with herbaceous plants, but there is a sufficient literature on trees to give a fairly clear concept of the factors and problems involved. Furthermore, there is very little reason to suppose that the principles concerned differ with the type of vegetation.

Plants frequently transpire very slowly even in a saturated atmosphere and, according to Darwin (*42*), leaves may continue to give off water into supersaturated air up to 5 percent above saturation, when transpiration becomes nil. But Seybold (*189, p. 92*) believes that transpiration must cease when the vapor-pressure potential is zero and states that transpiration is found in a saturated atmosphere only where the temperature conditions have not been carefully watched. Only when the leaf temperature is higher than that of the environment can transpiration into a saturated atmosphere occur. If the leaf has the same temperature as the external air, then transpiration into a saturated atmosphere is impossible.[4]

Thus, Dole (*52*) found the greatest transpiration in *Pinus strobus* when the humidity was lowest but, as previously stated, in such experiments one must be careful to watch both the light and the temperature as well as the other factors that commonly change with the humidity.

Cribbs (*40*), who found the relative humidity very important in his studies on the transpiration of *Tilia*, showed that *Tilia* transpired more as the general dryness of the habitat (site) increased.

AIR TEMPERATURE

Various authors have tried to devise formulas that would take into account the principal contributing factors associated with humidity, but up to the present none of these formulas is very applicable under practical field conditions. Of the many factors which influence

[4] This whole question of the relation between the water content and osmotic pressure of cells on the one hand and (1) the vapor pressure (relative humidity) of the surrounding atmosphere as well as (2) the corresponding water relations of the immediate environment (soil, air, or biotic) on the other has been discussed at considerable length with special reference to the ecology (xerophytism) of herbaceous vegetation by Walter (*224*) and Fukuda (*62*) under the name of the "Hydratur" of plants.

humidity, temperature and air movements are among the most important. The effect of temperature has been repeatedly mentioned: The higher the temperature with a given amount of moisture in the air, the lower the relative humidity, i. e., the higher the temperature, the more water vapor the air can contain before the saturation point is reached. The absolute humidity or total water content varies directly with the temperature, given an unlimited water supply, as does also the total amount that it is possible for air to contain before becoming saturated; but the relative humidity varies inversely with the temperature, the total water being constant.

Rubner (*178, p. 72*) has pointed out that the absolute humidity in a forest is not essentially different from that in the open, while the relative humidity, on the other hand, may be very different. Since the air temperature in a forest is generally considerably less than that in the open, especially in the summer, it follows that at different seasons the relative humidity must be considerably greater than in the open. For example, if the forest temperature is 15° C. while that in the open is 20°, when the relative humidity in the open is 70 percent, in the forest (even with the same absolute humidity) the relative humidity will be 94 percent.

SOIL TEMPERATURE

While Cribbs (*40*) showed a very close relation between soil temperature and transpiration in *Tilia*, the correlation between soil temperature and relative humidity is probably not so close, since the latter is affected more by the air temperature, which in turn is influenced only indirectly by the soil temperature.

Baldwin (*7*) found no direct relation between soil temperature at 1 foot and the evaporation as measured by atmometers in a 50-year-old stand of *Betula papyrifera* and *Pinus strobus* in New York. His data for this station are given in table 16.

TABLE 16.—*Weekly averages of temperature and evaporation in the open and in a 50-year-old stand of paper birch and white pine, 1932*

Period	Open				Woods	
	Rainfall	Air temperature, 7 a. m.	Soil temperature	Evaporation	Soil temperature	Evaporation
	Inches	*° F.*	*° F.*	*Cc*	*° F.*	*Cc*
June 27–July 3	0	----------	59.1	93	54.3	53
July 4–10	3.12	57.9	59.2	70	53.0	28
July 11–17	.41	56.8	62.0	115	55.1	58
July 18–24	2.67	56.5	63.0	96	55.6	45
July 25–31	2.62	58.8	63.3	75	56.4	17
Aug. 1–7	1.21	57.9	62.7	80	56.4	18
Aug. 8–14	1.46	56.3	62.4	72	57.5	33
Aug. 15–21	1.18	57.7	62.3	76	56.5	22
Aug. 22–28	.78	56.3	62.0	72	56.5	37
Total	13.45	458.20	556.0	749	501.3	311.0
Average	1.49	57.2	61.8	83.2	55.7	34.5

AIR MOVEMENTS

Air movements, as is to be expected, affect transpiration because they replace saturated air with nonsaturated air in the vicinity of the transpiring leaves. Wiesner (*239*) found in *Populus tremula* that

transpiration in a windy place was about twice what it was where there was no wind. Seybold (*189, p. 98*) in his rather extensive researches, found that in *Taxus baccata* and *Quercus ilex* the ratio of transpiration in a calm to that in a wind was 1:1.1 to 1.2. The effect of wind on transpiration seemed to be greater in leaves with cuticular transpiration than in leaves whose transpiration is primarily stomatal. In the latter case the transpiration from the cells is into the intercellular air spaces, while in the former the water loss is directly into the surrounding air; it is, therefore, natural to expect the effects produced by wind to appear more quickly in cuticular than in stomatal transpiration. This may explain the results of Fritzsche (*61*), who found that wind affects the transpiration of hardwoods more than that of conifers like spruce and fir, although Douglas fir occupies an intermediate position. In some species wind even tends to cause a closing of the stomata and a resultant decrease in transpiration; so that while wind may decrease the relative humidity, it does not necessarily increase the transpiration. Rubner points out also that relative humidity in forests is higher than in the open because of the decreased air movement; the trees tend to check exchanges between the interior of the woods and the air outside, although, to be sure, some diffusion always occurs.

Gail and Long (*64*) noted, in Idaho, that *Pinus contorta* was much more limited in its distribution than *P. ponderosa*, the former being restricted to the areas protected from the wind. When the effect of air movement on the transpiration rate was studied, it was found that the transpiration in *P. contorta* was increased by the wind more than four times as much as that of *P. ponderosa*, as seen in table 17. This is an interesting example of distribution influenced by transpiration rate as affected by wind.

TABLE 17.—*Effect of air movement on transpiration rate in two species of pine*

Species and air condition	Leaf area per gram, dry weight	Water lost per gram, dry weight	Water lost per gram, fresh weight	Water lost per square decimeter of leaf area	Increase in water loss in wind over that in still air on basis of leaf area
	Square decimeters	*Grams*	*Grams*	*Grams*	*Percent*
Pinus ponderosa:					
In still air	0.9270	11.53	3.56	12.31	18.85
In wind	.7692	13.86	5.25	14.63	
P. contorta:					
In still air	1.4780	9.26	2.35	6.71	74.98
In wind	1.0910	11.87	4.36	11.74	

Wind velocity in forests.—Schubert (*185*) (table 18) reported the wind velocities in an opening in a beech thicket 4 m high as compared with those in the surrounding open country.

TABLE 18.—*Wind velocities in an opening in a beech thicket and in open country*

Height above ground (meters)	Velocity per second		Ratio
	In open	In thicket	
	Meters	*Meters*	*Percent*
0.2	1.76	0.42	24
2.2	2.94	.37	13
4.2	3.85	.83	22

Geiger (*67*) recorded the following wind velocities in a 65-year-old pine forest, 15 to 16 m high, at different heights above the surface within the stand:

Height (meters):	*Wind velocity (meters per second)*
16.85	1.61
13.70	.90
10.55	.69
7.40	.67
4.25	.69
1.10	.60

According to these figures, there is very little decrease in the wind velocity between the bottom of the crowns at 11 m and the ground; only within a few centimeters of the ground is there any marked decrease in the strength of the wind. In the canopy (13.70 m) the wind increases about 40 percent, and a few meters above the crowns (16.85 m) it is two and one-half times as strong as within the stand (10.55 m).

Since the wind movements affect the transpiration and the humidity, it is not surprising that shaking of the leaves also affects transpiration. Stahl (*204*) found by weighing that the movement of the leaves of *Populus tremula* increases the transpiration. The water loss of leafy twigs that had been in steady movement was greater than that from twigs with fixed leaves, and in every case there was a significant decrease in water loss in the branches in which movement of the leaves was suppressed.

HUMIDITY IN FORESTS

Many papers have been written on the humidity within forests and the factors influencing it, with special reference to the problems associated with forests rather than to those that affect humidity everywhere, such as air movements and temperature. First may be mentioned changes of humidity with distance above the ground in forests. The humidity may be measured directly or, as is frequently done in ecological studies, the evaporation rate is measured by the use of Livingston atmometers. The humidity alone, as has been seen, does not determine the transpiration rate but must be considered along with other factors, such as light and temperature. A measurement of the evaporation rate is, therefore, of greater ecological significance, since in it these other factors are included.

The factors which vary with the evaporation rate have been studied especially by Burger (*25*), who found a very close correlation between evaporation from atmometers and the temperature, humidity, and hours of sunlight. There was, however, little correlation between wind and evaporation because of the fact that in times of wind there was likely to be an excess of humidity, a lower temperature, or an absence of light. This does not mean, therefore, that wind does not increase the evaporation but merely that over periods of time the amount of evaporation cannot be computed from the wind data with the same accuracy as from the light, temperature, and humidity figures.

Gates (*66*) studied the evaporation rate at various levels in different types of woods and under various ecological environments in Michigan. Although he did not place the atmometers one above the other in the same spot but scattered them over considerable territory, he found in pine woods, in general, that the evaporation rate increased with height

above the ground. In aspen woods where the atmometers were fairly close together he obtained the following results:

Height (meters):	*Evaporation rate compared with that at ground (=1)*
3.7	1.48
1.8	1.39
.9	1.16

Huber (*109*) found that in an oak crown in July, if Piche atmometers at 4 m from the ground show an evaporation of 100, then at 12 m the evaporation rate is 131. Likewise if the evaporation rate in May was 100 at 2 m from the ground, at 10 cm it was 2.9. The increase in rate between 10 cm and 2 m is seen to be, therefore, much more rapid near the ground than higher up in the canopy. Likewise Geiger (*67*) showed that in a pine stand there were differences of 25 percent in the relative humidity between the air above the forest floor and that above the crowns.

Thone (*212*) set up five atmometer stations on a transect through a hardwood hammock (in northern Florida) and two additional stations at heights of 4 and 18 m. His results are not very well summed up but, in general, he found that evaporation rates at the ground level were to those at 4 and 8 m about as 12:15:18.

Similarly Plitt and Pessin (*171*) found that the evaporation from a white spherical atmometer near an oak tree in a rather dense woods near Mount Desert, Maine, increased from about 431 cc at 1.5 m from the ground to about 487 cc at 6 m and to 738 cc at 9.5 m during 43 days in midsummer. Also there was much more variation with the exposure at the greater heights.

Allee (*3*) noted that the evaporation power of the air on the forest floor in the tropical rain forest of Panama was one-half that of the lower forest canopy and one-sixth that from the surface of a neighboring lake. Here conditions were very constant and the results are interesting from that point of view, although a discussion of conditions in tropical rain forests lies somewhat outside the scope of this review.

Within the crowns themselves there is a variation in the transpiring power. Thus Huber (*109*) found that if the evaporation rate inside an oak crown 4 m from the ground is 100, then at the edge of the crown it is 104; and Hanson (*83*) found that the evaporation at the south edge of crowns of *Ulmus*, *Acer*, *Tilia*, *Quercus*, and *Fraxinus* was one and one-half to two and one-third times that within the crowns, while the humidity within the crown was 1 to 6 percent higher than at the edge. Hanson is one of the few workers in this field who measured both the evaporating power and the humidity.

Since the temperature and rainfall show seasonal variations, it is not surprising to find that the humidity in forests also varies with the season. On the basis of Müttrich's observations (*160*) the average for the years 1886–90 in Prussia is shown in table 19.

TABLE 19.—*Relative humidity of air in the forest above that in the open, 1886–90*

Species and number of stands	Age or type of stands	Season			
		Spring	Summer	Fall	Winter
		Percent	*Percent*	*Percent*	*Percent*
Beech, 6	70–80 years	1.0	7.9	4.6	1.9
Spruce, 5	60–70 years	3.4	5.4	4.8	1.4
Pine, 4	Mixed ages	4.4	8.2	5.6	2.5
Pine, 1	Plantation	1.5	5.5	2.8	.9

The observations of Ebermayer, as recorded by Rubner (*178, p. 73*), for 1868–69 (table 20) give somewhat higher results.

TABLE 20.—*Relative humidity of air in the forest above that in the open, 1868–69*

Species and number of stands	Age of stands	Season			
		Spring	Summer	Fall	Winter
	Years	*Percent*	*Percent*	*Percent*	*Percent*
Beech, 2	60	5.3	12.9	3.7	2.4
Spruce, 2	40	7.9	10.7	9.1	6.8
Pine, 1	36	3.6	1.2	3.5	4.2

A similar table compiled by Toumey from Swiss and German observations (*215, p. 214*) gives the following figures (table 21):

TABLE 21.—*Excess of relative humidity in the forest over that in the open country, in percent of saturation*

Season	Beech	Spruce	Scotch pine	Larch
	Percent	*Percent*	*Percent*	*Percent*
Spring	1.91	6.92	2.93	2.83
Summer	9.35	8.56	3.87	7.85
Autumn	4.07	7.01	4.24	5.45
Winter	1.73	4.76	2.70	.34
Mean of year	4.27	6.81	3.44	4.12

It seems certain from these data that during the growing season there is an increase in the relative humidity in the forest. This cannot be considered as necessarily favorable, since too high relative humidity may check transpiration sufficiently to hinder growth. In high altitudes, high humidity may also lead to an excessive growth of lichens, but in the lower regions and in dry periods an increase in the relative humidity in the forest is, of course, favorable for the trees. This is especially important in spring (May) when the air is relatively the driest, as shown by the following figures from Bavaria: The relative humidity from March to August in the open was 81, 77, 67, 71, 72, and 73 percent for these respective months, while in the forest the humidity for these same months was 85, 82, 76, 80, 82, and 81 percent, respectively (*178, p. 73*).

In the forest during May, however, the relative humidity is nearly 10 percent higher than in the open. In Switzerland, April is the driest month, according to Bühler (*23*), who attributes the failure in many cases of natural reproduction in open old stands to the increased evaporation at this season. Spruce stands, since they are green all the year, show on the average a higher relative humidity throughout the year than deciduous beech stands. In the growing period, however, beech stands seem to have a higher relative humidity than spruce.

For various parts of Europe the differences in relative humidity within and outside of forests have been tabulated by Zon, as recorded by Toumey (*215, p. 213*). His figures are given in table 22, which shows that the relative humidity inside the forest is usually 3 to 10 percent greater than outside.

TABLE 22.—*Relative humidity outside and inside the forest, in percent of saturation*

Region	February–April		May–July		August–October		November–January		Entire year	
	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Mountains of Alsace	80	85	68	75	78	84	85	89	77	84
Bavaria	80	84	70	80	78	85	87	90	79	85
East Prussia	84	85	64	68	76	81	90	92	78	82

The forest litter also exercises an effect upon the relative humidity of forests, according to the researches of Ebermayer, as recorded by Morosov (*159, p. 175*), who found that the evaporation from the soil in stands not covered with litter was reduced 62 percent in comparison with soil outside the forest; but when the soil was protected by litter, then the evaporation is reduced 23 percent more, making a total reduction of 85 percent. In other words, if soil in a given period of time evaporates 100 units, the same soil under the forest canopy without litter would evaporate 38 units, and with litter only 15.

It is, therefore, easy to see that the especial conditions under the forest canopy bring about a strong decrease in the transpiration of the young growth and of the second story, and that the conditions under which the lower story develops are much moister than those under which the upper story is developing, as pointed out by Morosov (*159, p. 175*). The young growth, possessing leaves not so heavily cutinized and not so easily able to check transpiration, is thus developing in an atmosphere more nearly suited to it. Likewise, in clearings, the relative humidity is less than in the stand, generally being between that of the open country and the dense forest. Since the relative humidity in clearings is frequently 10 to 25 percent less than that below the forest canopy, when the mother trees are cut down the young growth, which has been forming only shade leaves up to the present time, is now suddenly plunged into a drier climate, so that the growth of the tender leaves is often seriously checked.

It is not surprising to learn, therefore, as reported by Adams (*2*), that thinning a 20-year-old white pine plantation so that the basal area was reduced 45 percent lowered the maximum relative humidity in the crowns 3 to 4 percent, caused a slight increase in the evaporation rate both in the crowns and near the ground, as measured by atmometers, and increased the daily wind movement three to four times in the crowns and two to three times at 8 inches above the ground.

Altitude affects the humidity of the forest. According to observations in Bavaria by Ebermayer, as stated by Rubner (*178, p. 74*), the annual relative humidity of forests at high elevations is greater than that in the lowlands. Also, in the high mountains the difference between the relative humidity in the open and that in the forest is greater, which is in agreement with the fact that the temperature differences between the forest and the open increase with altitude. This is of importance silviculturally, since in the higher altitudes the humidity is frequently excessive, and attention needs to be directed more in such cases to increasing the temperature which, of course, then results in the lowering of the relative humidity.

The ecological relations of trees centering around humidity have been hinted at above in the discussion of the work of Cribbs (*40*), but experimental studies were carried out by Weaver and Thiel (*230*), who studied the absolute and relative transpiration of seedlings of *Acer saccharinum* and *Quercus macrocarpa* which had been planted in pots and then placed in three different associations: (1) Prairie, (2) scrub, (3) woodland. Every 4 days the plants were changed from one site to another. In another series of researches, branches were cut from various types of trees (*Acer*, *Prunus*, *Ulmus*) and their transpiration studied by means of potometers. Results showed that evaporation and transpiration were greater in the prairie than in the scrub, but greater in the scrub than in the high forest.

Similar results are reported by Weaver. In one of his studies (*226*) he compared the evaporating power of the air in a Douglas fir and in an Engelmann spruce forest with that in more open communities. In the forests the water-holding capacity of the soil is increased by the duff and litter, which aids in conserving both winter and summer precipitation.

> The shade of the trees and various forest layers reduces the evaporating power of the air, while the water loss from the soil is further retarded by the layer of duff (*226*, *p. 108*).

Table 23 shows the average daily evaporating power of the air in the communities studied from June 10 to August 23. Likewise Weaver found that the evaporating power of the air in a chaparral thicket in Nebraska was only half of that 75 feet outside.

TABLE 23.—*Average daily evaporating power of air in communities of Douglas fir and Engelmann spruce, by weekly periods*

Period	Douglas fir	Engelmann spruce	Period	Douglas fir	Engelmann spruce
	Cc	*Cc*		*Cc*	*Cc*
June 10–17	28.8	21.6	July 22–29	11.3	8.5
June 17–24	11.1	7.1	July 29 to Aug. 5	16.0	11.4
June 24 to July 1	20.4	15.0	Aug. 5–12	8.6	6.2
July 1–8	15.2	11.1	Aug. 12–17	8.5	6.3
July 8–15	5.7	4.4	Aug. 17–23	11.6	8.8
July 15–22	6.1	5.2			

As has been frequently pointed out, the forest and its environment react reciprocally upon each other; the environment influences the forest and the forest in turn influences the environment. Similarly the excess humidity in forests may result in distinct structural changes in the leaves. Leaves growing in a very damp atmosphere are usually broader and thinner than those growing in dry surroundings, which tend to be more xeromorphic. It should be kept in mind, however, that if available water is present in the soil a decrease in the relative humidity of the atmosphere will not result in structures as xeromorphic as when available soil moisture also is lacking.

The relative humidity may affect not only the morphology of the leaf but also its physiology. Molisch (*154*) found that when leaves of plants growing in moist air were placed in air relatively dry, all or part of the leaves soon formed abscission layers and dropped off. This fall of the leaf may occur also in moist air when the soil moisture is insufficient. When air and soil dryness are united, the fall of the

leaves occurs still sooner. Molisch explained on this basis the fall of the leaves of young pines in times of drought. Autumnal abscission may be explained similarly. In the spring the tender needles transpire strongly when the roots are actively functioning and when there is plenty of soil moisture. In late fall, the decrease in soil moisture (associated with the temperature changes in the soil and air and the resulting alterations in the normal water intake and water loss) is one of the deciding factors in the autumnal drop of leaves.

The effect of forests on climate is still an unsettled question. While there seems little doubt that the local climate in forests is different from that outside, the extent of these effects on the large masses of surrounding air has been much disputed. Although this question lies outside the scope of this discussion, it may be mentioned that an extensive literature is available to the student of this subject.

Soil Moisture

Soil moisture, which depends upon rainfall and other climatic factors, in turn affects transpiration. It is to be expected that the more water is available the more will be absorbed and transpired by the local vegetation. Halbfass (*82*) estimated that in northern and central Germany at least 50 percent of the annual precipitation is accounted for by plant transpiration. Geinitz, according to Halbfass, had stated that 65 percent of the annual precipitation was transpired by the plants in Mecklenburg, but Halbfass found that only 54 percent could be thus accounted for in Sachsen-Weimar and thus derived his 50-percent figure from these two sets of data.

Hartig (*90*) was among the first workers to point out the increased transpiration with increased water content of the soil. Broad-leaved and coniferous trees, he found, decreased their transpiration as the soil moisture decreased. His work, however, as has been mentioned before, has little quantitative value. Von Höhnel (*100*), in his classic experiments, likewise found that after every watering his plants transpired more heavily the following day.

According to Stenström (*209*), it can be accepted as a general rule that, extreme cases aside, $\frac{B}{L}=T$ for any given plant, in which B=soil moisture, L=relative humidity of the air, and T=transpiration. In other words, the transpiration varies directly with the soil moisture and inversely with the relative humidity. This general rule has been made somewhat more inclusive by Gain (*65*), who states it thus: If the soil-moisture optimum is not exceeded, the amount of water transpired per unit surface is always greater in moist soils than in dry ones, but beyond the optimum water content transpiration decreases. In moist soils the daily transpiration curve goes relatively much higher than in dry soils; but plants on dry soils transpire relatively more at night.

Recent research papers in this field can be grouped either as ecological or physiological, depending on whether they rest on observations in the field or on experimental work in the laboratory. In the former category should be included the work of Cribbs (*40*), who found that the transpiration of *Tilia* was not much influenced on the various sites that he studied unless the soil moisture content was decreased to near the wilting coefficient. The daily decrease in transpiration which occurred in the afternoon was not due to low soil

moisture but to the inability of the plant to conduct water rapidly enough. The drop in transpiration occurring when the soil moisture reached the wilting coefficient was more permanent and was accompanied by visible wilting. The soil moisture in a region of ample precipitation is thus more likely to become a limiting factor in sand than in clay soils, since it is here much easier for the moisture content of sandy soils to get as low as the wilting coefficient.

Hendrickson (*93*), however, found in various *Prunus* orchards in California that the stomata were wider open on moist soils than on dry soils, indicating (not proving) that transpiration was taking place more rapidly.

A significant paper by Stanfield (*206*) in this connection illustrates the importance of the interpretation of data. He studied the osmotic pressure of *Pinus ponderosa* leaves from trees 4 to 6 feet high near Boulder, Colo., in an attempt to find whether the osmotic pressure was correlated with the evaporation rate (as measured by atmometers) as well as with the soil moisture and soil temperature. He found that the lowest relative humidity was accompanied by the highest osmotic pressure, and he seems to have concluded that the two are correlated. Since, however, the work of other research workers has shown that high transpiration rates are correlated with low relative humidities, it would necessarily follow that high transpiration rates are correlated with high osmotic pressures, which is a conclusion contrary to the results of most workers.

When Stanfield's data are carefully analyzed, however, it is found that the contradiction is more apparent than real. It is unfortunate that he did not measure the transpiration rates of the trees studied, for if he had he would probably have found a low transpiration rate. His results simply mean that in the comparatively dry atmosphere of Colorado the trees studied reduced their transpiration, and this reduction of transpiration was associated with the high osmotic pressures of the needles. The highest osmotic pressure was found in July, which is also the season of lowest relative humidity. Stanfield also reported that there was no correlation between the osmotic pressure and the soil moisture; but if his data are examined closely, it will be noted that the highest osmotic pressure during the time of his studies occurred either in July when the soil moisture was at a minimum, or in May when the soil temperature was lowest (and the soil moisture, consequently, unavailable). The literature is very often confused in this fashion by workers who apparently have too narrow a knowledge of the field and of the problems involved to interpret their results correctly.

Experimental work in this field is perhaps more conclusive. Bader (*5*) found that transpiration in various species of *Pinus* was directly related to soil moisture, which, along with light, was the chief controlling factor. In transpiration intensity the pines studied fell into three groups:

(1) Highest: *P. excelsa* Wall., *P. cembra*, *P. peuce* Griseb.
(2) Middle: *P. sylvestris*, *P. montana* Mill.
(3) Lowest: *P. austriaca* Höss., *P. strobus*.

The morning drop in transpiration occurs more quickly in the more rapidly transpiring species.

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Shreve (*192*) studied the effect of soil moisture on the transpiration and the size of the stomatal openings in potted plants of *Parkinsonia microphylla* Torr. The water content of the soil was decreased from 15.1 percent to 3.5 percent, or 76.8 percent of the original amount, which led to a lowering of the relative transpiration (in the sense of Livingston) of 98.4 percent. In another plant, lowering of the soil moisture from 14.5 percent to 3.4 percent, i. e., 76.5 percent of the original water content, lowered the relative transpiration 97.2 percent. In this latter case the average diameter of the stomatal openings in the drier soil was only one-seventh of that in the moister soil.

Bates (*11*) studied the transpiration of two sets of potted trees at a water content of 9.05 percent and then raised the water content of one set to 12 percent, which brought about a remarkable increase in the transpiration, as follows:

	Percent
Ponderosa pine	34. 4
Douglas fir	30. 5
Lodgepole pine	33. 9
Engelmann spruce	8. 8
Bristlecone pine	14. 5

This increase in transpiration is especially noteworthy since the wilting coefficient of 4.88 percent was never closely approached. This study of Bates is frequently referred to in the literature, because he included in his paper a very comprehensive group of silvicultural factors in order to correlate the natural distribution of the common conifers in Colorado with the climatic factors and to show that the natural distribution in that region was distinctly based upon specific adaptations, especially to the water relations. He correlated the transpiration with the water requirement, sap density, wind, light, temperature, etc., in an attempt to show that the water relations of the various species in regard to these factors were specific, permitting the species to grow in the particular locations where found. The chief criticisms of his work are that it is too comprehensive in that it tries to consider too many changing factors at the same time, and that too few examples were used in each experiment. In many cases only two plants were used; and it is very unfortunate that work which has been cited so frequently should be based upon so few data. It should be added, however, that most of his conclusions have been supported by other workers who devoted their attention to special phases of the problem and examined each of these more exhaustively.

Pearson (*167*) carried on a somewhat similar experiment with potted conifers of Arizona and New Mexico. The wilting coefficient of the soil was 10.5 percent; and after the seedlings were planted enough water was added to bring the soil moisture to 20 percent. After this soil-moisture content had been maintained for several months, watering was discontinued in one series of pots; the transpiration rate began to fall immediately, and at the end of a month in most cases, it was less than 3 percent of normal. The soil moisture, during this time, had fallen to 0.2 to 0.5 percent above the wilting coefficient. During the next 2 months the transpiration was almost imperceptible, although the plants did not seem to be wilting. When changed from the outdoors (32° F.) to the greenhouse (54°) no appreciable increase in transpiration occurred. To learn whether the plants were really living, two of the pots containing yellow pine were watered at the end of 3 months, which restored the moisture content

to 20 percent. Immediately the transpiration rate increased to the normal before the water supply was cut off, and a month later new shoots appeared. This is a remarkable example of the way in which plants are able to check their water loss through transpiration to adapt themselves to a decreased water supply, but, unfortunately, not all plants are able to adapt themselves so efficiently to an unfavorable soil-moisture content.

Dole (*52*) found with 3-year-old potted plants of *Pinus contorta* that transpiration, when the soil-moisture content is 20 percent, is two to seven times as much as when the soil-moisture content is only 10 percent, in the case of sandy loam. Büsgen and Münch (*33, p. 304*) report that ash used 56,689 kg of water per 100 g of leaf substance when given just enough water to remain alive and 100,077 kg when watered abundantly. Corresponding figures for pine were 5,802 and 12,105 kg.

The studies on soil-moisture content as related to transpiration have been summed up by Baker (*6, p. 48*) and indicate that:

1. In the presence of plentiful soil moisture—
   (*a*) transpiration falls when stomata close on account of the darkness of night;
   (*b*) during daylight hours transpiration is closely correlated with the same factors as influence evaporation.
2. With deficiency of soil moisture—
   (*a*) transpiration falls on account of stomatal closure;
   (*b*) transpiration also falls even if stomata remain open, due to some form of mechanical or physiological control.

COMPOSITION OF SOIL SOLUTION

Not only is the quantity of soil water important, but the composition also may affect transpiration. Of the various common soil-water components only two, humins and salts, will be mentioned here, these because of their silvicultural importance. In most forest soils there is an extremely high percentage of organic matter in various stages of decomposition. To test the effect of these humous compounds on transpiration, 50 g of humus was mixed with 500 g of distilled water and filtered. In the filtrate, which contained 0.041 percent of organic substance and 0.018 percent of inorganic materials, were placed some herbaceous plants, as well as branches of *Taxus*. All showed a decrease in transpiration of 10 to 30 percent compared with plants in distilled water, as reported by Burgerstein (*28, p. 147*).

The effect of composition of soil water on the transpiration of trees has been very little studied. There have been, however, many papers on the effect of salt on the transpiration of herbaceous plants, most of which indicate that an increase in salt content decreases the transpiration. Various reasons have been assigned for this, all of which may play a role, but doubtless the most important factor is the change in osmotic pressure. Materials which increase the osmotic concentration of the cell sap decrease the ease with which water can be withdrawn, and consequently they decrease the transpiration.

Minor Factors

AIR PRESSURE

Among the minor factors that have been studied in connection with the transpiration of trees is air pressure. Variations in air pressure at any one spot are so slight as to be negligible in transpiration studies; but if one wishes to compare transpiration values at different altitudes,

air pressure cannot be neglected. At sea level the barometer reading is about 760 mm, while at 1,000 m it is 600 mm, and at 6,000 m only 300 mm. The evaporation rate (i. e., from atmometers) at 1,000 m is about 25 percent more than at sea level and at 6,000 m about two and one-half times as much. It is, therefore, obvious that at higher elevations, other things being equal, transpiration will be increased. It is, however, very difficult to separate the altitude effect from the other factors concerned, because at these different altitudes there are always differences in relative humidity, temperature, light intensity, etc. Renner (*175*), however, carried on some experimental work to show the effect on transpiration of the decreased atmospheric pressure with the results shown in table 24.

TABLE 24.—*Effect on transpiration of decreased atmospheric pressure*

Air pressure (millimeters of mercury)	Relative increase in transpiration	Relative decrease in pressure
734	1	1
508	1.34	1.44
381	1.39	1.99

Shreve (*194*) determined, by means of the cobalt paper method, the relative transpiring power of 30 perennials of various biological types, including *Prosopis juliflora velutina* Sarg., at different altitudes in the Santa Catalina Mountains of Arizona. He found the maximum transpiring power was later in the day as the elevation increased. In the case of the mesquite (*Prosopis*) at 2,400 feet, the relative transpiration was greatest at 8 a. m., i. e., the leaf behaved most like a free water surface at this time and differed least from the atmometer. At 4,400 feet the maximum transpiring power was at 10 a. m., while at 5,000 feet, it occurred at 11 a. m.

ETHER AND VOLATILE OILS

Jumelle (*117*) showed that leaves of *Quercus*, *Ostrya*, and *Fagus* always transpired more in an atmosphere containing ether when in the light, but in the dark the transpiration of the anesthetized leaves was always less than that of untreated ones. Other workers, however, have found that ether always increases transpiration. This would seem to be more reasonable, since it is known that ether increases the permeability of cells, and materials which increase cell permeability favor transpiration.

The effect of volatile oils is more important from a silvicultural point of view, inasmuch as such substances occur in nature. Many plants exude volatile oils, which increase the total gas pressure and decrease the conductivity of the air to radiation. This had, therefore, appeared to earlier authors as an adaptation to dry environments, the best known examples among trees being *Eucalyptus* species; later researches, however, have shown that plants which give off volatile oils are not characteristic of any particular ecological environment but are found as frequently in moist places as in dry ones. Marloth (*147*) mentions that the Mediterranean region and the deserts of north Africa, Asia, and California contain many plants which are oil-bearing; but he also calls attention to the fact that many other

regions contain this same type of plant and, furthermore, states that the oil, to which is due the aromatic odors of these plants, is commonly given off more in damp and foggy weather than in dry weather. It is his opinion that these substances are a protection against animals rather than against drying out.

It is the opinion of the writer, however, that ecologists very commonly make mistakes when they try to explain all similar phenomena in the same way. It is quite possible that desert plants are aided in their struggle to retain water by the same substances that keep plants in moist conditions from being eaten by animals. If the gas pressure and the insulating effect of the air surrounding the leaf are increased, transpiration will be diminished; but whether this is an "adaptation" is quite a different matter.

Griffon (*73*) calls attention to the fact that, contrary to popular opinion, eucalyptus transpires less than other common trees of France, such as poplar, willow, linden, and walnut. Its use in plantings to dry up marshes and swampy regions is effective not because of its high transpiration rate but because it produces much foliage quickly.

CARBON DIOXIDE

Of the other various components of the atmosphere which influence transpiration only two are of sufficient importance to warrant inclusion in this review: carbon dioxide and sulphur dioxide. The proportion of CO_2 in the atmosphere is very small (only 3 parts in 10,000), but at the same time it is very constant; changes in this percentage occur rather rarely and under exceptional conditions. Soil bacteria sometimes increase noticeably the percentage of CO_2 in the soil air spaces and also in the soil water. Likewise, vegetation on a forest floor, as well as the forest vegetation itself, may locally increase the percentage of CO_2 in the atmosphere of forests at night when photosynthesis is no longer taking place. These increases, however, are seldom large and are consequently probably unimportant as far as transpiration is concerned, since they occur at a time when transpiration is already decidedly checked.

In the small amount of experimental work that has been done on this subject with woody plants, it has been noted that transpiration in air free of CO_2 is always greater than that in air containing CO_2, and when the CO_2 content is relatively high transpiration is decidedly depressed. The common explanation for this is that the stomata tend to close in an atmosphere containing excessive amounts of CO_2. This is true, but it is also well known that the main function of stomata is to permit CO_2 to enter the leaf so that it may be used in photosynthesis. If CO_2 caused the stomata to close, the leaf would not function. The truth of the situation seems to be that as the CO_2 is manufactured into food in the guard cells of the leaf their turgor increases and the stomatal openings enlarge, permitting more CO_2 to enter, especially in light. It is also true, however, that in pure CO_2 or in air extremely rich in this compound the stomata close, so that the decrease in transpiration in the presence of excessive amounts of CO^2 may be explained by the smaller stomatal openings. And still another reason for the decrease in transpiration in atmospheres high in CO^2, in the opinion of the writer, may be sought in the fact that the CO_2 is combined with the water in the cells to form organic foods.

The more CO_2 is present, the more water molecules are combined to form foods, and the less is the amount of water available for transpiration. At the same time the osmotic pressure of the cell sap is increasing.

It has been noted by Kosaroff (*130*) that CO_2 also depresses transpiration when present in large quantities around the roots. He grew plants in flasks with enough water present for growth and conducted CO_2 through the flasks (containing the roots), measuring the transpiration by weighing. When pure CO_2 was led through the flasks, transpiration was lowered about half. When a gas mixture of 80 to 90 percent of CO_2 and 20 to 10 percent of oxygen was put into the flasks, the decrease in transpiration was not so pronounced, leading Kosaroff to the conclusion that CO_2 had both a direct and indirect effect on the water relations, the former being due to the specific effect of CO_2 and the latter to the deprivation of oxygen. The depressing action of CO_2 was shown not only in decreased absorption but also in decreased transpiration. The dissolved CO_2 depressed not only the activity of the root cells but, as it penetrated into the plant, affected also the stomata. As has been stated above, however, since the amount of CO_2 present either in the soil or in the air does not change very much in nature, the effect of CO_2 is probably not of great importance from the point of view of silviculture.

SULPHUR DIOXIDE

Sulphur dioxide is important in connection with silviculture chiefly through the addition of this gas to the air in the vicinity of smelters, certain types of factories, etc. The question of smelter-smoke damage is one appearing frequently in the literature, and there is now little doubt of the harmfulness of this compound on vegetation. Schröder (*183*) studied especially the effect of SO_2 on the water relations of plants, which he found lost the ability to transpire normally when in an atmosphere of 0.02- to 0.10-volume percent SO_2. In some cases cut twigs and in others rooted plants of *Acer platanoides*, *Castanea vesca*, *Fagus sylvatica*, *Quercus*, and *Abies pectinata* were studied. As a result of the decreased transpiration, less water is absorbed and the general nutrition of the plant is thus thrown out of balance. He found also that the effect of SO_2 on transpiration varied fairly directly with the amount of SO_2 present. In the presence of light, high air temperature, and low relative humidity more SO_2 was taken in by the plants with more serious after effects than in the dark, at low temperatures, and in humid air. He also noticed that the transpiration of conifers is not so visibly depressed as is that of broad-leaved trees in air containing equal amounts of SO_2, which he thought entered the leaf not only through the stomata but also through the cuticle.

In other experiments, Schröder and Reuss (*184*) studied the effect of relatively high concentrations of SO_2. Three similar twigs of *Acer platanoides*, A, B, and C, were treated in the following fashion: A was put into an atmosphere containing no SO_2; B in an atmosphere containing 1 part SO_2 in 8,300 of air; and C in an atmosphere containing 1 part SO_2 in 1,666 of air. During the following 46 hours A transpired 25.19 g per 1,000 cm^2; B, 18.62 g; and C, 13.85 g.

Oliver (*165, pp. 26–28*), using a potometer, placed twigs of *Acer pseudo platanus* in containers in which various amounts of SO_2 were introduced. At a concentration of 1 part SO_2 to 13,300 of air (i. e., 0.6 mg of SO_2 per cubic foot) there was a sudden depression of the water absorption, and at a concentration of 1 part in 6,700 the transpiration was very considerably lowered.

Although Wieler (*236*), using twigs of various woody plants, and Stoklasa (*211*), using small trees of *Picea excelsa*, did not find any depression in transpiration through the influence of SO_2, their results are quite contrary to those already mentioned and also to the results of Neger and Lakon (*161*), who repeated (apparently more carefully) the experiments of Wieler and came to the conclusion that SO_2 hindered photosynthesis and was directly toxic to the plant. Also, when the transpiration of healthy trees (*Acer platanoides, Picea excelsa, Pinus strobus*) was compared with that of trees that had been damaged by SO_2, both the water intake and the transpiration were found to be lowered in the latter. Their conclusion, therefore, is that under the influence of SO_2, as soon as the assimilation apparatus has been injured, a decrease in water absorption occurs which is often much greater than the decrease in transpiration, with the result that the leaves dry up.

Schröder and Reuss (*184*) found that a leafy branch of *Acer platanoides* which was not subject to SO_2 absorbed 26 g of water and gave off 33.05 g, while a twig which had stood for 6 hours in an atmosphere containing 1 part of SO_2 in 1,000 of air absorbed 12.6 g and gave off 8.15 g; the latter thus absorbed about one-half as much water as the healthy twig and transpired only about one-fourth of the amount. Neger and Lakon, who carefully copied this experiment, found, in general agreement with Schröder and Reuss, that the water absorption and transpiration of twigs exposed to SO_2 were much less than those of healthy twigs; but in both twigs there was a small increase in weight, which they explain by the fact that the experiment was performed under bell jars where transpiration was decreased. According to Schröder and Reuss, only the twig exposed to SO_2 increased in weight, but if that were actually the case, Neger and Lakon point out it would be hard to explain why the leaves exposed to SO_2 in the open should so soon have the appearance of dried leaves. The decrease in transpiration brought about by SO_2 is probably explained as due to injury to the guard cells and the consequent closing of the stomata, although this point has not been thoroughly cleared up.

POSITION OF LEAVES ON THE STEM

Certain factors which influence transpiration can hardly be classed as either internal or external but are really a combination of the two. In this category may be placed the position of the leaves on the stem. Lower leaves not only have different internal physiological relations from the upper ones but they are also placed in a different environment. Huber (*104*) has studied this question more intensely than anyone else. Twigs were cut off at various heights (2, 4, 6, 8, 10, 12, 14 m) from a tree of *Sequoia washingtoniana* (Wins.) Sudw. 15 m high and then placed in the same environment (not in water) and weighed at hourly intervals. In all cases there was a decided falling off in the transpiration rate with increasing stem level, so that the transpiration of the lowest twigs was, in certain cases, six times as great as that of

twigs from the 12-m level. In one series the hourly loss of water varied at different heights as follows:

Height (meters):	*Loss per gram of fresh weight in milligrams*
2	29
4	27
6	15
8	15
10	10
12	7
14	14

The cause of this lies not in differences in structure but in the greater difficulty of supplying water to the upper part of the tree owing to the resistance offered to the transpiration stream by the water-conducting tissues. The transpiration of the twig immediately after it is cut from the tree is generally greater than it is a few hours after cutting. The transpiration rate falls off rapidly at first and then slowly approaches a constant value, which apparently corresponds with the purely physical cuticular evaporation as opposed to the physiologically regulated stomatal transpiration at the start.

Later, Huber (*108*) studied the fall in transpiration with increasing height in many other trees, including *Fagus*, *Tilia*, *Picea*, *Acer*, *Quercus*, *Fraxinus*, *Larix*, and *Pinus*, all of which showed a decrease in transpiration rate with height above ground. Beech leaves, for example, taken from the tree at 20 m from the ground, transpired less than half as fast as leaves from a height of 10 m. In a still later paper (*110*) Huber showed that the transpiration of mesophytic, tolerant trees decreased with height more than that of intolerant ones. Thus, there was a greater decrease in *Sequoia*, *Tilia*, *Fagus*, and *Picea*, than in *Acer*, *Quercus*, and *Fraxinus;* and the decrease in *Larix* and *Pinus* was still less. Blaydes (*17*) also found with *Fagus* and *Carya* that the transpiration rate from leaves 4 feet above the ground was much greater than that from leaves 20 to 30 feet above the ground.

TRANSPIRATION AS A FUNCTION

No discussion of transpiration could be considered complete without reference to the question of the value of, or reason for, transpiration. The early students of plant physiology considered that transpiration, like photosynthesis and respiration, was a function, that is, it served some useful purpose in the life of the plant. In recent years, however, there has arisen a decided reaction against this point of view, and there are many workers who consider that transpiration is only a necessary evil. The leaf is constructed to manufacture food. Moist cell surfaces which permit the exchange of gases necessarily permit water vapor to escape—an inevitable result of the leaf structure and not in any sense purposeful.

Those who hold that transpiration fulfills a useful function believe that the transpiration stream aids in the distribution of minerals throughout the plant. Water absorbed by the roots carries with it the essential minerals, which flow along with the transpiration stream to the different organs of the plant; therefore, the more transpiration, the more water is carried from the roots to the leaves and the greater the amount and the speed with which the minerals are distributed.

The opponents of this view base their opinion for the most part on work done with herbaceous plants; and it may be that in these smaller forms diffusion processes are quite sufficient to satisfy the metabolic needs without the use of the transpiration stream. Haberlandt (*80*), pointing to the luxuriance of tropical vegetation, calls attention to the fact that here, where many of the largest trees are found, the transpiration rate is at a minimum and cites this as proof of the fact that a rapid transpiration stream is not essential for the growth of luxuriant vegetation. While he admits that the transpiration stream may help somewhat in the transport of nutrients, he believes that it is not the most important agent. The supporters of the functional hypothesis, on the other hand, call attention to the fact that while the transpiration stream in tropical trees is not rapid, it is very continuous and during the lifetime of the plant enormous amounts of water pass through in this fashion.

One does not need, however, to turn to tropical vegetation to find abundant proof of the relation between transpiration and mineral content. Stahl (*204*) reports that in *Populus tremula*, where the motion of the leaves increases the transpiration rate, there is also an increase in the mineral content of the leaves.

Ebermayer (*56*) even felt so sure of the relation between transpiration and the mineral consumption that he believed the water demands can be deduced from the ash content. In support of these views he found that the leaves of plants which transpire more rapidly, such as ashes, willows, alders, maples, and elms, contained the most ash (7 to 10 percent); while hornbeam, oak, and beech leaves showed only 4 to 5 percent; silver fir, spruce, and larch 2.9 to 3.5 percent; and forms demanding very little water, such as Austrian pine and Scotch pine, 1.3 to 2 percent.

Huber (*104*), in his work on differences in transpiration with differences in level in *Sequoia*, found a distinct parallelism between the decrease in transpiration rate and decrease in ash content in twigs from increasing heights. Sample data are given in table 25. The figures from the twig at 10 m do not seem to fit in with the others, but it is noteworthy that both the transpiration and the ash content in that particular twig were exceptionally high.

TABLE 25.—*Relation between transpiration rate (based on fresh weight) and ash content (based on dry weight) of Sequoia twigs at different elevations above the ground*

Elevation (meters)	Transpiration rate	Ash content	Elevation (meters)	Transpiration rate	Ash content
	Percent	*Percent*		*Percent*	*Percent*
2	100	100	10	91	90
4	91	82	12	57	70
6	69	72	14	53	85
8	68	74			

Burns (*29*), in work in Vermont with white pine seedlings, noted that those seedlings 8 to 10 weeks old which grew in full sunlight transpired 21 times as much as those in full shade, while those in half shade transpired 8 times as much as those in full shade. The dry weights per average of 1,000 seedlings and the ash percentages (based on dry weight) were as shown in table 26.

TABLE 26.—*Average dry weight and ash content of 1,000 white pine seedlings under different light intensities*

Light condition	Dry weight	Total ash	Ash content
	Grams	*Grams*	*Percent*
No shade	0.063	0.005	8.29
Half shade	.034	.003	9.35
Full shade	.010	.001	10.20

It is thus seen that the plants in no shade transpired 21 times as much water but accumulated only 5 times as much ash as those in full shade. The amount of ash, therefore, increases with the transpiration but not directly, indicating that the minerals are not absorbed passively along with the water but are regulated in their entrance by forces within the plant.

Whatever may be the effect of transpiration on the ash content, most workers are agreed that transpiration helps to lower the leaf temperature, which otherwise, in full sunlight, might get dangerously high. Thus Copeland (*38*), to cite a recent publication, found that the leaves of transpiring chaparral plants in California showed a temperature of 4° to 10° C. lower than the surrounding air. The temperature was lowered more when the under surface of the leaf was exposed, permitting free transpiration, than when the upper surface was exposed. Furthermore, species which transpired less rapidly showed less cooling effect.[5]

As to whether or not transpiration is a genuine function, it is the opinion of the writer that although a certain percentage of transpiration is possibly a necessary evil, transpiration does help the plant in that it cools the leaf mechanism and that it aids (even if it is not absolutely necessary for) the diffusion of mineral substances throughout the plant. Herbaceous plants might perhaps get along without the aid of the transpiration stream through root pressure, diffusion, capillarity, osmotic pressure, and other physical forces acting within the plant; but to distribute efficiently to the tops of tall trees the necessary supply of mineral salts is a somewhat different matter. Diffusion processes are not very rapid under such circumstances, and the bulk of evidence points to the fact that for a normal development of plant organs, as well as for the transport of minerals, the transpiration stream is of great importance.

SUMMARY AND SUGGESTIONS FOR RESEARCH

While some water is lost under abnormal or exceptional conditions by bleeding and guttation, most of the water is lost through the stomata of the leaves during the process of transpiration. The number and location of the stomata influence this loss and there are also specific and individual differences among trees, but the chief variations in losses are associated with environmental factors, such as light, temperature, humidity, soil moisture, etc.

[5] Many other papers written from a purely physiological point of view and dealing mostly with herbaceous forms tend to show the cooling effect of transpiration.

Need for further study has been indicated at various places in the body of the discussion, but several lines of work seem especially promising:

(1) Is the size of the vessels of the wood a good index to the water demands of a tree? Can the size of the vessels of the same species in various sites be taken as an index to the site possibilities, and are the sizes of the vessels in different species on the same site indicative of the relative water demands on that site? If so, a study of wood and root anatomy in this connection would give valuable results as to site adaptations.

(2) It should also be advantageous to know more about the water relations in various forest soils of the country. Not only their water content at various seasons of the year and at various depths should be more carefully studied, but also their wilting coefficients. Since plants do not wilt much until the wilting coefficient of the soil is reached, it would be advantageous to know over a period of years how many months of the year and in what seasons the soil-moisture content approaches the wilting coefficient.

Such information in connection with the water requirements of individual species should prove valuable not only in planning long-time planting projects over extensive regions, but also in local problems of seeding, rejuvenation, and management. Why are some trees able to withstand apparent droughts and seemingly unfavorable conditions so much better than others? If more were known about the internal anatomy of the tree in relation to its immediate external environment (air and soil), we should be able to give more satisfactory answers to these problems than at present.

(3) There is need also for more extensive work on the role of transpiration. It should be settled once and for all whether transpiration in trees aids in the absorption of minerals from the soil and whether plants that have high rates of transpiration utilize more soil salts than others. It is possible that, owing to the method of water translocation and the physical problems connected therewith, trees behave in this respect differently from shrubs and herbs. If it can be established that there is a connection between water requirements and mineral intake, with a resultant effect upon the soil mineral content, an important advance will be made. Not only would this provide silviculture with an easily measurable index to the relative water requirements of different species on the same site, but it would also shed some light on the general mineral needs of forest trees.

"ADAPTATIONS" OF TREES TO DRY CONDITIONS

For many years it was thought that plants living in dry regions transpired less than those in moister localities; and in xerophytes transpiration was thought to be at a minimum. Maximov, however, has done much to modify this opinion. His views on this subject have been summarized in book form (*148*); but the essence of Maximov's contributions has been stated also in more concise articles (*149*). According to him, plants commonly called xerophytes may transpire more intensely than many mesophytes, and the real essence of xerophytism is the ability to exist in arid regions regardless of the amount of water lost.

It has been pointed out that trees are seldom, if ever, found in genuinely arid situations, and they are included for the most part, therefore, in the group of mesophytes. Some, however, are able to endure greater extremes of drought than others, and, from a silvicultural point of view, the reasons for these differences are extremely important. While it is well known that certain species of trees thrive on comparatively dry sites and others demand a high soil-moisture content, the fundamental reasons for these differences have not yet been thoroughly explained. We know that all trees reduce the water content of a given soil to approximately the same wilting coefficient. Also, we know that conifers, in general, transpire more slowly per unit of leaf area than do hardwoods, and further that there is a relation between the osmotic pressure of the cell sap and both the water-absorption and water-retention capacities.

The distribution of species in relation to the moisture supply is one of the fundamental problems of ecology and will continue for some time to receive the attention of investigators in this field. Why are plants distributed over the surface of the earth in the particular way that they are found at the present time? Apparently, in the evolution of species, certain types have been able to survive in drier or moister regions and in the course of time have become adapted to these particular localities. In general, as has already been shown, temperature and moisture (by which is meant not only soil moisture but also the relative humidity) are the two most decisive factors in determining the distribution of vegetation.

Shreve (*195*) considered that the moisture ratio, or the ratio of the evaporation rate, as determined by atmometers, to the soil moisture $\left(\frac{E}{SM}\right)$ was an excellent single expression to show the combined effects of both air and soil moisture. The lower the ratio, the more favorable are the conditions. In studying the distribution of species in the Coast Range of California, he found that this ratio was 10 times as great in chaparral as in redwood forests and about 5 times as great at 5,000 feet as at sea level. The vegetation in this section was determined by (1) the seaward and landward exposure, (2) the altitude, (3) slope exposure, (4) topographic irregularity, and (5) proximity to the sea; but it will be noted that these factors are important mostly because of their effect (either direct or indirect) upon the water relations.

Similarly Cooper (*37*) found that the distribution of oak, willow, and chaparral associations near San Francisco Bay are determined largely by the interrelations of these various factors, the most important being topography, the soil, and the water table.

Various methods have been employed by ecologists for determining quickly and easily the type of vegetation which one may expect to find in a given locality. Shreve settled on the soil moisture ratio as a simple criterion. Others have worked in the other direction and have tried by some simple plant measurement to tell what the ecological conditions were.

Huber (*105*) determined the degree of succulence of the vegetation as the ratio of the surface of the leaves expressed in square centimeters to the volume of the leaf expressed in cubic centimeters. On this basis

he ranked plants in the following order, it being understood that the larger is this fraction, the more water-demanding are the plants:

	Ratio
Fagus sylvatica (shade)	153
Larix europaea DC	133
Fagus sylvatica (sun)	123
Quercus pedunculata (shade)	109
Q. cerris L. (young leaves)	88
Q. pedunculata (sun)	84
Betula verrucosa	84
Quercus ilex (greenhouse)	70
Abies pectinata (shade)	70
Pinus austriaca	44
P. cembra	44
P. montana	42
Picea excelsa (shade)	40
Ilex aquifolium	40
Abies pectinata (light)	39
Picea excelsa (light)	30

It is considered, therefore, that the problem at the present time is to learn what the climatic conditions are in the various regions on the surface of the earth and to correlate these with the vegetation growing there. It can then be determined where these species may be expected to grow outside of their natural range.

Thus Whitfield (*233*), studying the vegetation of the Pike's Peak section, found that *Pinus ponderosa* and *Pseudotsuga taxifolia* dominate the montane region while *Picea engelmanni*, *Populus tremuloides*, and *Pinus aristata* are most important in the subalpine. At progressively higher elevations, both the air and soil temperature decrease, while the rainfall and relative humidity increase. In the montane zone the transpiration is accordingly higher than in the subalpine, although lower than in the plain below. These results agree with those found in general in mountains.

Boysen-Jensen (*19*) took as his criterion the value of the relative transpiration, it being understood that the smaller is this value the more control the plant exercises over its transpiration and the drier the natural habitat in which it might be expected to survive.

On this basis Stocker (*210*) has assembled the transpiration data from different parts of the earth and from various ecological regions and has found that in general the relative transpiration of plant formations is about as follows (in percent): Water plants, 27; swamp and marsh plants, 16; plants of tropical rain forests, 13; mesophytes of the Temperate Zone, 12; desert plants, 10; heath and bog plants, 5.

Apparently, drought resistance may be attained in many different ways. According to Kearney and Shantz (*120*), plants may be classified as drought-escaping, drought-evading, drought-enduring, and drought-resisting.

Drought-escaping plants are those temporary annuals which develop and mature very rapidly in periods when soil moisture is abundant. They have, therefore, no methods of conserving moisture. The drought-enduring plants are desert shrubs which, in times of drought, shed their leaves, and go into a sort of dormancy when the soil moisture reaches the wilting coefficient. Drought-resisting plants are the succulents which have provisions for storing water, united with arrangements for its conservation. Drought-evading plants are those which delay the ultimate exhaustion of a limited water supply by their economic utilization of the supply.

While some forest trees store water and are thus drought-resisting, and others, e. g., deciduous trees, drop their leaves and thus show drought-enduring characteristics, most forest trees come in the class of drought evaders. The methods by which they evade drought are extremely complex and may be tabulated as follows:

1. Preventing heavy losses of water:
   - *a.* Reducing transpiring area:
     1. Reducing size and number of leaves.
     2. Increasing volume in relation to the surface—thick leaves.
   - *b.* Reducing transpiration rate:
     1. Changing position and curling.
     2. Changing surface structure:
        - *a.* Thickening of cuticle and outer epidermal walls—sun leaves.
        - *b.* Wax and resin.
        - *c.* Hairs.
     3. Changing cell sap concentration.
     4. Forming buds in the petioles.
     5. Changes in stomata:
        - *a.* In number.
        - *b.* In structure and location.
        - *c.* In function or movement.
2. Assuring adequate supply:
   - *a.* By increasing size and depth of root system.
   - *b.* By displacing water from one organ to another or from stored regions.
   - *c.* Absorption by aerial organs.
3. Using water efficiently—Low water requirement.

The methods outlined above will now be discussed in some detail. Any or all of them may be combined in the same plant. It is, therefore, not possible to say that any one factor is responsible for the development of a tree in any particular dry area. Also different trees in the same area may have different methods of protecting themselves against dry weather, i. e., evading drought, as cited by Baker (*6, p. 63*). In the central Rocky Mountains, white fir and aspen grow in dense stands on the best sites and, when mature, have about the same height. On dry sites in the same region the aspen is reduced to dense thickets of trees only 8 to 10 feet tall, while the white fir maintains its height of 60 to 70 feet, although the trees in such circumstances are much more widely spaced. The aspen has maintained itself by reducing the transpiring area, while the fir has increased the absorbing area per tree.

METHODS OF CHECKING TRANSPIRATION

Of the trees which reduce the number of leaves, *Parkinsonia* in the southwestern United States is one of the best examples. In this genus practically all of the photosynthesis is carried on by the green stems, and the leaves here are truly conspicuous by their absence; from the striking green stems and branches, the tree has received its common name "palo verde" (or "green pole").

The autumnal fall of leaves in broad-leaved trees is also a phase of reduction in transpiring surface to meet the reduced water supply. It is well known that in periods of excessive drought many leaves are dropped. That this decrease in transpiring area is associated more with moisture than with temperature is shown also by the fact that trees in warm climates with a rainy and dry season lose their leaves during the dry period. Holtermann (*102*) studied this question in Ceylon, and came to the conclusion that the fall of leaves depends entirely upon rainfall, as shown by the fact that the leaves of

endemic species always fall in dry periods. This question was also studied by Kamerling (*118*) who cut off leafy twigs from various species in Java and compared the transpiration of those leaves which ordinarily are shed during the dry periods with those which are not. On the average the trees which shed their leaves during droughts showed a much stronger transpiration and were less able to regulate their transpiration than the trees which retained their leaves in dry periods.

Increase in volume at the expense of surface or the development of succulence is of very slight importance in trees, but it has been noted that the mesophyll is commonly more compact in trees in arid regions. In *Eucalyptus*, for instance, the leaf tissues of the species found along river banks and in humid valleys generally have a much larger proportion of intercellular space than those of species which grow in drier regions. These differences in structure are obviously related to the sun and shade differences previously mentioned.

A change of position in leaves in the light is also seen in *Eucalyptus* species, many of which place the leaves in a vertical position when exposed to light, as opposed to the horizontal position of normal leaves. Certain species of *Acacia* behave similarly, and the forests of Australia, where these genera are common, are sometimes spoken of as "shadeless". The vertical leaves of *Eucalyptus globulus*, however, have a structure somewhat different from that of the horizontal ones. The former have a thick cuticle, while the latter have a more waxy coating, according to Johnson (*116*), who also reports that, contrary to common opinion, the vertical leaves transpire more than do the horizontal ones. Since most workers have held a different view, this problem apparently deserves further study.

Trees that come more within the scope of this publication are the juniper and linden. Stahl (*202*) calls attention to the fact that in *Juniperus virginiana* L., in sunny sites the scales are shorter and more closely appressed, while in shady habitats or in the interior of the tree, the scales are more leaflike and more loosely grouped together. A similar condition is cited by Kerner (*121*), who states that the leaves of *Tilia alba* Michx. and *T. tomentosa* Moench have an almost vertical position on branches and twigs exposed to the sun; but in shaded regions, the leaves remain much more nearly horizontal. The curling up of the edges of leaves at the beginning of wilting is a very common occurrence and probably protects the tissues somewhat against further drying out.

Another common protection against excessive transpiration is the thickening of the cuticle and of the outer epidermal walls, resulting frequently in leaves that are tough or leatherlike. This is often seen in broad-leaved evergreens and is probably a protection against the physiological dryness of the winter season. This thickening of the walls of the epidermis sometimes proceeds so far that all that remains of the cell lumen is merely a point, as in Scotch pine, or only a thin line, as in the mountain pine.

The cuticle also may be covered with wax, forming a shiny, smooth layer as in *Quercus sessiliflora*, or with a dull covering as in *Q. pedunculata*. This type of protection is quite common also in broad-leaved evergreens as well as in conifers. The *glauca* varieties of conifers are so called from the bluish-white waxy bloom on the leaves. Many trees, such as *Salix fragilis* L., *Amygdalus communis* L., and *Acer*

pseudoplatanus have the wax coating only on the under side, which is normally away from the sun; and many workers have questioned the drought-evading value of the wax in this location. Kerner, however, has pointed out that even in a slight wind these leaves are turned so that the under side is at least partly in the light, and he considers that such coverings, even though on the under side, are of distinct advantage.

To show experimentally the value of the waxy covering in checking transpiration, Tschirch (*216*) removed the wax from one of a pair of leaves of *Eucalyptus globulus* and found that after 24 hours, the leaf with the wax removed had lost 59.7 percent of the contained water, while the control leaf with the wax still on it had lost only 42.2 percent.

As has previously been seen, young leaves in which the cuticle is not well developed transpire very freely; it is, therefore, not surprising that buds are commonly protected against water loss by waxy coatings, and that the bud scales protect the tender leaves beneath from water loss and other injuries has long been known. In the winter in Siberia, in buds of woody plants (including *Malus baccata* Borkh., *Betula alba* L.) the danger of drying out is overcome by a strong cutinization, thick hairs, and waxy excretions of the bud scales, as pointed out by Schostakowitsch (*180*).

To test experimentally the protection provided by the bud scales against transpiration in winter, Wiegand (*234*) cut off the scales from buds of various trees (*Pinus laricio*, *Aesculus hippocastanum*) and a part of the naked buds he then smeared with varnish. But as Burgerstein (*28, p. 197*) has pointed out, it would have been much better to have compared buds with and without their scales, especially if one wishes to learn something about their behavior under natural conditions.

Hairs are found especially on broad-leaved evergreens and under conditions such as those occurring in semiarid regions. According to Kerner, there is not a single family of plants found in the Mediterranean region which does not have some genera whose leaves are provided with a heavy coating of hairs. Here, also, in many cases the hairs are found chiefly on the under side, but the same argument applies as in the case of waxy coatings, according to Kerner, who states that the slightest movement of air turns these leaves toward the light. In the opinion of the writer, however, Kerner has emphasized too much the light relation. In some of these instances the leaves do not have to be turned in order for the hairs on the lower side to serve as a protection against excessive transpiration, inasmuch as they may protect against wind as well as against sunlight. Although the importance of hairs in checking transpiration has probably been somewhat exaggerated, as pointed out by Sayre (*179*), they are probably more of a protection against wind when on the lower side than when on the upper side, which may explain their survival on leaves of such trees as *Populus alba* L., *Salix caprea* L., *Sorbus aria* Crantz, and *Alnus rugosa* Spreng. As pointed out above, hairs are also present in buds, where they are sometimes strongly developed. In beech, sycamore, and other cases they may disappear later, being retained only in the angles of the leaf veins. Brenner (*21*) found in various oaks an increase in hairiness with an increase in insolation, which is in agreement with the fact that in the mountains of central and southern Europe, where an alpine vegetation is found, the number of forms with

woolly and silky leaves increases on the southern slopes and in proportion to their dryness.

In the section dealing with the effects of temperature and moisture on water content, the correlative changes in osmotic pressure of the cell sap were noted. Cells with high osmotic concentration are not so permeable to water, and plants in dry localities commonly have a high concentration of sap in the leaf cells. Which is cause and which is effect in this case is not so easy to determine. Do the plants have a high concentration of cell sap in order to check transpiration, or has the excessive transpiration resulted in an increase of the osmotic pressure of cells? The two effects are probably simultaneous and reciprocal. This is an excellent illustration of the fact that an unfavorable environment may cause a reaction in the plant which checks the unfavorable effect.

Other substances in the cell, in addition to salts, may check transpiration. Among these may be latex, since, as Volkens (*222*) points out, the number of plants with milky juice is relatively high in hot and dry climates. It might also be mentioned that, among the maples, the only one with a milky sap is the Norway maple, which grows in soil physiologically drier than the other maples.

To tannins also has been attributed the function of checking transpiration. The leaves of evergreen plants must lower their transpiration as much as possible, and Fleischer (*59*) considers that the tannins which are present in almost all evergreen leaves, especially in the epidermis, are a protection against drying out in winter. Volkens (*222*) points out that tannins are also common in desert plants.

The value of tannins in checking transpiration has been questioned by Wisser (*243*), who pressed the sap from the leaves of plants rich in tannins and compared the evaporation rate of this sap with that of distilled water; he found that the cell sap evaporated 93 to 99 percent as rapidly as the distilled water, which would seem to indicate that the tannins are not such a good protection against transpiration as others have thought. It should be pointed out, however, that Wisser's test is not a particularly good one. When whole cells are squeezed, one gets not only the water from the vacuole but also from the protoplasm, and the concentration of the tannin would consequently be less in the pressed product than in the vacuoles of the living cells.

An especial protection against strong evaporation is the formation of buds inside the base of the petioles, as in *Philadelphus* and *Platanus*, to which Wiesner (*240*) first called attention. According to him, also, the terminal buds of many species of *Acer* are protected in a similar way against drying out, since here the bud remains protected for a long time by the base of the two top leaves. Also, the stipules commonly protect the young, tender leaves of the bud from excessive water losses. Interesting in this connection is *Liriodendron tulipifera* L.; here the two relatively large, shield-shaped stipules are so placed that they form a kind of sack, in which the foliage leaf grows protected as in a sort of chamber until the epidermal cells have become thickened enough so that there is no longer any danger of drying out, when the two stipules separate and fall off.

Plants growing in dry habitats show fewer stomata than those growing in moister regions. Czech (*41*) found that species growing in wet sites had more stomata per square millimeter than related

species of the same genus in dry sites, e. g., *Populus nigra* had 135 stomata per square millimeter, while *P. alba* had 315.

Brenner (*21*) found that leaves of *Quercus pedunculata* on the drier sites of southern Europe had considerably fewer stomata per unit area than those on the moister sites of central Europe.

Hirano (*96*), in studying the water relations of stomata in about 40 varieties of *Citrus* in California, found that the number of stomata was more closely related to the rainfall during the spring months when the leaves were developing than to the total annual rainfall or to light and temperature. The hardier varieties, it should be noted, also were characterized by a low stomatal density.

Although Eberhardt (*54*) found in *Salix* and *Populus* that as the relative humidity increased the stomata became fewer but larger, most workers have found an increase in stomata in moist regions, all other factors being equal. We have learned, however, that sun leaves frequently have more stomata than shade leaves if there is an abundant moisture supply. In considerations of stomatal numbers, as elsewhere, simultaneous consideration of temperature, water, and light is important. No one factor in silviculture can be considered without taking into account the other two.

Changes in number of stomata in dry regions are frequently associated with changes in structure. In conifers, the stomata are very frequently clogged up with waxy granules similar to those on the epidermis. Wulff (*244*) noted also in *Betula alba* that where this tree grows as a shrub on the dry, wind-blown sands of Spitzbergen, the stomata on the under side were filled with large, shiny, brown granules of wax, while the leaves of similar species in the botanical garden at Lund showed no wax deposits. The stomata may also be plugged up by the adjoining parenchyma cells, which sometimes grow inward in such a fashion as to close the stomata; this has been noted in old leaves of *Camellia japonica* L. and *Prunus laurocerasus* L. by Schwendener (*187*).

CONTROL BY STOMATA

The stomata are of prime importance in controlling transpiration, however, through the movements of their guard cells. When conditions are favorable for photosynthesis and there is plenty of light, moisture, and CO_2, the guard cells, which also contain chlorophyll, manufacture carbohydrates; and the increased osmotic pressure results, owing to their peculiar morphology, in a wider opening between them. This permits CO_2 to enter easily to the mesophyll cells below and at the same time permits water vapor to pass outward. If any of the conditions for optimum photosynthesis are lacking, such as insufficient light or water, the stomata then tend to close, serving somewhat as automatic regulators. This was the accepted view for many years, but in 1908 Lloyd (*139*) published a comprehensive monograph in which he questioned the regulatory function of the stomata. He worked chiefly on desert plants, and furthermore his methods have been questioned by Loftfield (*140*) and others, so that his attempt to discredit stomatal regulation of transpiration in mesophytes has met with a rather hostile reception; the conclusion at the present time seems to be that while the stomata perhaps do not regulate the transpiration so accurately or completely as was once supposed, they are able to regulate water losses to an appreciable and valuable extent.

One of the difficulties has been to measure accurately the stomatal openings. Of the various methods devised, four have been used profitably by various investigators. These are (1) direct observation, (2) porometers and stomatographs, (3) fixation, and (4) infiltration. The direct observation of uninjured leaves under the microscope would appear to be the simplest and most reliable method, but it is generally difficult to apply, because of the small size of the stomata and the opaqueness of the leaves. Such studies also must be carried on in situ, which adds to the difficulty of the observations. Some workers have tried to strip the epidermis from the leaves in the field and observe directly with the microscope; but such manipulation runs the danger of injuring the stomata in the process of stripping.

The porometer, as devised by Darwin and Pertz (*44*) and improved by Knight (*124*) rests on the principle that changes in stomatal width can be registered by changes in the velocity of an air stream forced through the leaf. It consists essentially of a T-tube, the lower end of which rests in a vessel of water (or mercury). One of the arms of the T-tube ends in an open rubber which can be clamped off; the other ends in a small funnel which may be glued or attached to a leaf. Through the open tube, water is drawn into the stem of the T-tube, and the open tube is then clamped off. The pressure of the column of water in the stem of the tube tends to draw in air through the leaf, and the rate at which the water column drops is taken as an index of the condition of the stomata. If the stomata are completely closed the water column remains at the height to which it was originally raised or changes its position very slowly, but if the stomata are wide open, the water column falls rapidly. Furthermore Darwin (*43*) checked the accuracy of the porometer by weighing, and showed that in *Prunus laurocerasus* there is an agreement between the water losses and the size of the stomatal opening; the water loss varies with the square root of the porometer readings.[6]

In the fixation method as devised by Lloyd (*139*), the epidermis is removed as quickly as possible and plunged into absolute alcohol, fixing the stomata. This method has some of the disadvantages of the direct method, and the whole operation must be done very rapidly. It is also very important that a great many measurements be carried out because of the sources of error involved. Other students have used other fixatives, such as picric acid, but the principle is the same.

The infiltration or injection method of Molisch (*155*) is simpler and better adapted for use under natural conditions than some of the previous methods, but it also has its shortcomings. This method depends upon the fact that absolute alcohol placed on the epidermis of a leaf penetrates only wide-open stomata, resulting in the appearance of dark spots in the vicinity. If the stomata are nearly closed, the alcohol cannot penetrate and infiltration does not occur; but other liquids, such as benzol and xylol, can penetrate even partially closed stomata. All that is needed for this method, then, are three bottles containing absolute alcohol, benzol, and xylol, respectively, and appropriate brushes or rods. First the alcohol is applied to the leaf and, if it penetrates, the stomata are wide open; if benzol enters but not the alcohol, the stomata are only partly open; if only xylol enters the leaf, the stomata are nearly closed; while if none of the liquids

[6] A self-registering modification of the porometer is Balls' stomatograph (*8*), for a description of which the reader is referred to the original literature.

enter, the stomata are completely closed. Other workers use other injection materials but the same principles apply.

FACTORS INFLUENCING STOMATAL MOVEMENTS

Factors other than soil moisture and humidity influence the movements of the stomata, but since the movements affect transpiration, no matter what may be their origin, it will not be out of place to mention some of these factors. The stomata are completely movable only in mature leaves. When young, the stomata tend to close or open only under especially favorable conditions. The leaves nearest to the base are generally the first to have movable stomata. As the leaves become advanced in age the stomata lose their mobility, and in evergreen leaves (or needles) that remain on the trees for several years the mobility may completely cease, as shown by the studies of Dengler (*45*) and others. In older leaves the walls of the guard cells become somewhat lignified, and it is this lignification doubtless which checks their mobility. This hardening of the guard cells has been reported in conifers by Noack (*162*) and others as well as in *Laurus nobilis* L. and *Quercus ilex* by Von Guttenberg (*77*).

Likewise, the stomata in autumnal leaves, especially after the photosynthetic function has ceased, have been shown by Stahl (*203*) to be closed. Even some of the willows, which ordinarily do not close their stomata when wilting, showed a decrease in the size of the openings in late summer. Similar results are reported by Molisch (*156*) and Burgerstein (*27*), who found in plants with green leaves on one side and yellow leaves on the other that in the former the stomata were open, while in the latter they were closed, exceptions being *Populus alba* and some *Salix* species, where the yellow leaves also showed open stomata.

About half an hour after twigs are cut and placed in water the stomata tend to close, as pointed out by Huber (*104*). This effect of cutting on the closing of the stomata is, of course, a source of error in work based upon cut twigs and should be taken into account in any absolute measurements attempted by this method.

As is to be expected when the real function of stomata is considered, light influences their behavior. The stomatal opening should be wide enough to admit sufficient CO_2 and yet not so wide as to permit excessive water losses. These two requirements are often contradictory and result in a compromise. Since the supply of CO_2 is of use to the plant only when in the light, the width of the stomata must depend in the first place on illumination. Light, therefore, causes the stomatal opening to be wider and darkness causes it to be narrower. Thus Sitton (*196*) found that the stomata of pecan leaves opened very soon after exposure to direct sunlight and closed soon after being shaded. Also the stomata on completely shaded leaves in the interior of the trees were not open.

The stomata are generally most widely open between 11 a. m. and 3 p. m., while at night or on dull days they may be completely closed. On the other hand, if the darkness is unduly prolonged, the stomata may reopen to permit the entrance of oxygen. This had been shown by Dengler (*45*) to be the case in conifers, by Weber (*231*) in *Aesculus*, and by Magness and Furr (*145*) in apple trees, to cite only a few of the papers on this subject.

Trees show specific differences in their ability to close their stomata under unfavorable conditions. In some species the stomata are much more adjustable than in others. Thus, in the aspen, which generally occurs on wet soil but is able to live on comparatively dry soil, the stomata close completely when water shortage occurs. The willows, on the other hand, are generally forced to live in more moist habitats because they lack the power to close their stomata rapidly. Similarly the stomata of trees of tropical rain forests show little mobility, according to observations of Shreve in Jamaica (*193*).

Betula alba and *Alnus glutinosa*, according to Büsgen and Münch (*33, p. 217*), also are unable to regulate their transpiration appreciably through stomatal movements, and it is noteworthy that these plants are confined to fairly moist habitats, although Burgerstein (*27*) states that *Alnus* and *Betula* close their stomata very quickly when the water supply begins to fail.

The water supply and the humidity are, along with the light, by far the most important factors governing stomatal behavior. Neger and Lakon (*161*) found in 1-year-old needles of *Abies*, *Picea*, and *Tsuga* that the stomata were open when the leaves were in a fresh condition and closed when wilted. Similar results were obtained by Dengler. In fact, most of the workers who have studied this question have come to the conclusion that excessive losses of water are associated with closure of the stomata.

While most of the work on this subject has been done with herbaceous plants, many papers have appeared dealing with trees, especially horticultural species. Hendrickson (*93*), using the fixation method, found the maximum stomatal opening in *Prunus* at 9 a. m. until 12 noon and the minimum at 8 to 11 p. m. In the shade the maximum opening occurred later in the day. The stomatal behavior was correlated with the temperature and humidity and also with the soil moisture. The stomata, however, did not vary in the width of their openings with the soil moisture until the soil-water content approached the wilting coefficient. In some species, due to insufficient conductivity of the tissues, the leaves began to decrease in water content early in the morning; this is the probable cause of the closure of the stomata in the early afternoon, which permits partial replenishment of the water lost. Similar results were reported by Veihmeyer and Hendrickson (*220*).

Magness and Furr (*145*), in their work on apple leaves, reported very similar results. On dry, warm days the stomata close in the middle of the day regardless of the soil-moisture supply. They likewise report that the stomata were not affected by soil moisture until the wilting coefficient was reached, and consider the condition of the stomata to be an excellent way of determining whether the tree is getting sufficient moisture. Sitton (*196*) observed similar behavior in pecans.

Burgerstein (*27*), who studied the relation between wilting and the closing of the stomata on 140 species of trees, found that wilting resulted in complete closure in 56 percent, partial closure in 34 percent, and no marked change in 10 percent of the species. He found also that wilting affected the closure of stomata in a higher percentage of trees than of herbs.

Since light and moisture are the important factors determining stomatal behavior, it is natural to expect a seasonal effect: the stomata

are more nearly closed in winter than in summer, and those of nearly all evergreen shrubs and trees close early in the autumn when the available water supply commences to be diminished, according to Büsgen and Münch (*83, p. 218*). If cut twigs of *Ilex* or *Taxus*, however, are placed in water in a warm room, the stomata reopen in *Ilex* within a few hours and in *Taxus* within a week.

Weber (*231*) studied the condition of the stomata on two trees of *Aesculus hippocastanum* in Austria over an entire growing period, using the infiltration method. His results do not disagree with those of other workers, but it would seem impossible to draw any very valuable conclusions from two trees even though many observations were made on each tree.

This entire relation of the stomata to water and light has been very well summed up in the work of Stålfelt (*205*), who carried out many observations on *Picea excelsa* in the field, measuring the effect of light and water on the stomata at different hours of the day and under different external conditions. He concluded that the behavior of the stomata is conditioned by three separate systems, which he calls the "passive", the "photo-active", and the "hydro-active", all three being related to the water content of the plant. When there is plenty of water the guard cells of the stomata open "passively", due to their internal osmotic properties. The "photo-active" system results from the effect of light either on the osmotic substances within the guard cells or from a more direct stimulating effect. When water is at an optimum, the stomata are very sensitive to light, and under these conditions there is a delicate balance between the passive and the photo-active effects. When the water content becomes suboptimal the stomatal movement is dominated largely by the "hydro-active" system and the stomatal cells then play an active part. As the water content continues to fall below the optimum there comes a time when the photo-active and the hydro-active systems are balanced as to their importance in the regulation of the stomatal opening. In general, this means that when there is plenty of water, light is the dominant controlling factor, but when water is lacking, light becomes secondary. Most of the relations between light and water discussed above can be fitted into this picture. We thus see why it takes some little time for the stomata to close even after wilting has commenced; light and water are acting in opposing directions. Likewise, the temporary widening of the stomatal aperture, which frequently precedes the decrease of transpiration during wilting, may possibly be explained by opposing hydro-active and passive effects. The opening of the stomata at the close of wilting, commonly found in dried-up leaves, is also probably a passive posthumous effect.

Before closing this subject of adaptations to drought, in view of the economic importance in silviculture of our coniferous species it may be well to cite some of the special adaptations to the diminished water supply exhibited by these forms. Attention has been called already to the waxy coatings commonly present, as well as to the thickenings of the epidermal cells, which in some cases reduce the lumina to almost nothing. These epidermal cells are generally stiff and hard, and towards the interior of the leaf they are frequently adjoined by similar thick-walled hypodermal cells, which also protect the interior of the leaf from water losses. This may explain the variability of their occurrence with the moisture of the habitat, as pointed

out by Stahl (*202*). In the needles of many species of fir growing in the sun, these hard cells form an almost continuous layer beneath the upper epidermis; while in the shade they are only slightly developed. Likewise, species of southern origin, e. g., *Abies cephalonica* Loud., show a stronger development of the hard cells than those in moister, more northerly regions, and the leaves of silver fir seedlings in the shade where there is plenty of water have almost no hard cells; while Groom (*74*) called attention to the xerophytic structure of the leaves of northern conifers, which live in regions where there is plenty of moisture but where, owing to the extreme cold, it is for the most part unavailable (physiologically dry habitats).

In his paper on the relation of the leaf structure of western conifers to light and moisture, Larson (*132*) compared the general shape of the leaf, shape of the stomatal depressions, location of the stomata in relation to grooves, nature of the parenchyma, ratio of the xylem to the entire leaf, amount of xylem per stoma, amount and condition of intercellular spaces, and presence or absence of endodermis and degree of its lignification, in *Tsuga heterophylla* Sarg., *Picea engelmanni*, *Abies grandis*, *Pseudotsuga taxifolia*, *Pinus monticola* D. Don., *P. contorta murrayana* Engelm., *P. ponderosa*, and *P. albicaulis*. His results show distinctly the relation of structure to tolerance and moisture requirements. Unfortunately, in this work the effects of light and moisture have not been separated, but on the other hand, as has so frequently been observed, these two factors are very difficult to separate ecologically.

METHODS OF ASSURING AN ADEQUATE WATER SUPPLY

INCREASING THE ROOT SYSTEM

Turning now to the methods by which plants might assure an adequate supply of water in their leaves, the most obvious method would be that of expanding the root system. But, on closer observation, it will be seen that to expand the root system in times of drought or when the water supply is endangered is somewhat like lifting oneself by one's bootstraps. The roots cannot grow unless they have food and water, both of which presuppose a supply of water. It is true that roots are positively hydrotropic and will follow up a gradually receding water supply, but this is a somewhat different matter.

While, as we have seen from the work of Schröder (*182*), leaves do not begin to die until they have lost 50 to 80 percent of their water, roots show signs of water deficiency when the leaves have lost only 40 percent of their water. Evidently roots are more sensitive to drought than are the leaves, possibly because they are nearer the source of supply and consequently are the first to feel the effects of drought.

Dingler (*47*) determined the transpiring area of the leaves of a 7-year-old potted plant of *Acer platanoides* to be 906 cm^2, while the size of the entire root surface was 1,720 cm^2, that of the absorbing roots being 1,000 cm^2. Such calculations are, however, of little value since neither the area of the root hairs is considered nor that of the mesophyll cells where the actual transpiration occurs.

The depth to which roots will go when soil conditions will permit them is, in some cases, astonishing. Renner (*176*) reported that when the Suez Canal was dug, roots of tamarisks were found 30 m from

the surface. While it is true that a root system is modified somewhat by the water conditions, it is also true that the size and form of root systems are probably determined more by soil conditions and the inherent nature of the plant than by the water relations, which are inconstant and vary markedly from place to place even within narrow geographical limits.

STORING AND DISPLACING OF WATER

The storage of water to avoid drought is characteristic of succulents (drought-resistant plants) rather than of trees, although, as has been pointed out, the water in tree trunks, as well as that in the larger roots, serves to some extent as a daily reservoir. Living wood may contain 70 percent and more of water, and losses during dry periods, as well as those caused by daily transpiration excesses, may be replaced from the amount stored in the stem and roots. That tree stems behave as water reservoirs and change in size accordingly has been shown by the work of MacDougal (*142*, *143*), who measured the daily variations in circumference of trees in the southwestern United States by means of special apparatus (dendrograph); in practically all of the species measured, circumferences were found to be greater at night and less in the daytime.

When the soil-moisture content reaches a critical minimum, plants are able to withdraw water from one cell or organ to supply another. Thus the mucilaginous cells in the leaves of *Quercus pedunculata*, birches, and willows may serve as a supply of water to the adjacent cells. When water is plentiful the cells absorb water and retain it, and when a shortage of water sets in these cells sink together as the mesophyll takes water from them. According to the calculations of Haberlandt (*81*) the quantity of water liberated by the collapse of these cells to one-half of their original volume can supply the water transpired by a horsechestnut leaf for more than 2 hours and by pear trees for 39 minutes.

That the demands of the leaves seem to have precedence in the water supply of the tree is indicated by the work of Bartholomew (*9*), who showed that detached lemon twigs with fruits attached wilted much less in a unit of time than did those without fruits. At the same time, the attached fruits decreased in diameter two to three times as much as did detached fruits. Although the leaves on the tree do not wilt until the wilting coefficient is reached, the fruits suffer long before the soil moisture has reached this critical minimum. Similar results were reported by MacDougal (*142*) with walnuts in Arizona.

It is also interesting to note that when some of the leaves are removed from a rapidly transpiring tree, the remaining leaves may increase their transpiration rate, as reported by Hartig (*91*) in a 5-year-old potted spruce plant. When all of the needles were present on the tree the leaves transpired at the rate of 270 g per square meter of leaf surface. When 40, 70, and 90 percent of the needles had been removed, those remaining transpired at the rate of 272, 460, and 607 g per square meter, respectively.

Plants are not only able to transfer water from one organ to another, but they are also able to transfer it from moist soil to dry soil, according to Breazeale and Crider (*20*). Working with catclaw, date palm, the orange tree, tesota, palo verde, mesquite, and other plants, these workers found that the roots could penetrate soils that were below the

wilting point and transport to this dry soil the moisture obtained in a moister soil horizon. It is even possible for a deep-rooted plant to absorb moisture from the subsoil, transport it to a drier soil, and there give it up, where it may be absorbed by a shallow-rooted plant. The part this process plays in desert associations and its practical importance remain for future research to determine.

ABSORBING OF WATER BY AERIAL ORGANS

Still another method of providing for water is absorption by aerial organs. Actual absorption of dew by leaves is very slight, although Spalding (*199*, *200*) reported that leaves of *Celtis*, *Parkinsonia*, *Prosopis*, and others are able to absorb water vapor from very humid atmospheres. The same may be said of the absorption of rain by leaves and twigs. Although these organs are able to absorb water to a slight extent, they certainly are not able to absorb water as easily as they can lose it. The chief value of rain probably lies in the checking of transpiration rather than in the absolute amounts of rain water absorbed by the aerial organs of the plant.

In this connection one might mention the interesting modification possessed by some shrubs and trees of semiarid regions, such as *Tamarisk* spp., which, according to Volkens (*223*), absorb water from the atmosphere with the aid of hygroscopic salts that they secrete and then pass this absorbed water on to the tissues beneath. But it must be admitted that an osmotic system which would permit of this sort of transfer is rather difficult to understand.

TESTING ABILITY OF TREES TO WITHSTAND DROUGHT

It is, of course, advantageous to know as much as possible concerning the drought resistance of trees at various stages, especially when plantings in regions where the water supply is limited (i. e., semiarid regions) are contemplated. Much information has been obtained empirically in the past (*173*) simply by noting whether or not trees will survive in a given climate, but such methods leave much to be desired. For this reason recent workers have been attempting to obtain experimental data by subjecting plants to a lack of moisture and noting how well they survive. Among the recent students of drought resistance, Russian investigators have been notably prominent and the reader is referred especially to the works of Kondo (*128*) and of Tumanov (*217*), who have been chiefly interested in wilting as an index to drought resistance.

This entire problem, of course, is connected with the question of relation of species or variety to site and is of great practical importance in the matter of land utilization in general and of the best use of forest properties in particular. Although this matter has been dealt with in various places above, it is of such a fundamental nature that it cannot be stressed too much. Not only is there a difference in water requirement and drought resistence between species, but there may even be a difference between races of the same species. Thus Puttendörfer (*172*) attempted to find differences between three races of *Pinus sylvestris* from the Union of Soviet Socialist Republics, Germany, and France by studying (1) wilting, (2) water content of needles, and (3) osmotic pressure of needle press juice. Differences were greater in

respect to (3) than to either (2) or (1), the latter being the most unsatisfactory of the methods tried.

Other workers have devised special apparatus for creating an artificial drought in the laboratory in order to test the drought resistance of potted plants (tree seedlings). Thus Shirley (*191*) developed a desiccating chamber with a constant (or nearly so) saturation deficit, in which plants are left until dead. The length of time the plants survive and the soil-moisture content at death are used as criteria of the drought resistance. With this apparatus, Shirley[7] determined that of four species of seedling conifers tested, jack pine was the most drought resistant, followed by Norway pine, white pine, and white spruce. A more elaborate apparatus, in which heated air is forced over the plants, has been described by Aamodt (*1*).

SUMMARY AND SUGGESTIONS FOR RESEARCH

Trees growing under dry conditions seem to be able to adapt themselves thereto (within certain narrow limits) either by checking their transpiration water losses or by providing for an adequate water supply. The transpiration losses are checked largely through changes in the stomata, which serve (inadequately in most cases) to control the transpiration, although if the water supply remains insufficient for an extended period no amount of stomatal control can keep the plant from ultimately dying.

Under unfavorable conditions, however, trees may be able to survive if they have a root system sufficiently extensive to reach moist soil, if they have some water stored within them, or if they possess any other means of conserving or adding to their water supply. Herbaceous forms and xerophytes have many such methods, such as the production of mucilages (pentosans) and other water-holding colloids, but the (mesophytic) trees of the Temperate Zone (i. e., the forms here under consideration) seem to have few such additional means to insure their survival.

In view of the importance of planting drought-resistant species in regions where the water supply is below the optimum for most tree species, it is extremely urgent to know more about what qualities make for drought resistance and what species possess these qualities to the greatest degree. Also there is evidence that relative drought resistance varies with age, soil composition, etc., so that an exhaustive study now needs to be made of the relative drought resistance of our various economic species and of the factors with which this drought resistance may vary. There is thus evidence that seedlings have very special problems and that the difficulties involved in starting plantations in regions of suboptimum moisture are very different from those involved in growing or maintaining middle-aged and old stands in these same regions. In such regions the interrelations between site and species become especially important. Not only may the tree change its drought resistance properties as it grows older, but also as the root system enlarges the available water supply may increase. The development of our knowledge of this interrelation between the growing tree and its site consequently opens up a very large field for future research, where much work remains to be done.

[7] Unpublished manuscript

WATER CONSUMPTION BY TREES

All of the preceding work provides a basis for a discussion of the crux of the problem: How much water do trees really need? What are their actual minimum and optimum water demands? Methods of measuring water consumption, as found in the literature are, in general, three, which may be outlined as follows:

1. Transpiration per unit leaf area from specimens (*a*) in pots, or (*b*) cut from trees and applied to large trees in the open;
2. Transpiration per unit mass of leaves based on (*a*) fresh weight or (*b*) dry weight; these also may be taken from potted plants or from cut twigs and then applied to entire stands or individual trees;
3. Water consumption (mostly transpiration) per unit of total dry matter—water requirement.

The term "water requirement", introduced by Briggs and Shantz (*22*), as used here does not mean the water consumption referred to leaf area or mass but to the total dry matter produced by the plant. Forests are crops, and the silviculturist is interested in knowing how many grams of water are required to produce a gram of crop material.

These various methods of calculating water consumption have their advantages and disadvantages, which should be considered in determining the value of a given piece of work. In calculating the needs of a stand or of a crop grown under field conditions from pot experiments, certain deviations are to be expected. Briggs and Shantz (*22*) found that the water requirement of field crops was a bit higher than the figures as determined from potted plants, while Leather (*134*) found, in India, that the water requirement of crops grown under field conditions was generally lower than that of the same crops as determined from pot experiments. Since anything which affects the growth rate will affect the water requirement, these differences are not surprising. On poor soils and under poor nutrient conditions, plants will require more water to produce a unit of increment in a given time. It is, therefore, difficult to establish comparable water requirements unless the growth conditions are accurately defined. Also the fact that young plants have juvenile leaves less able to control water losses should be taken into consideration.

Transpiration, as has been seen, is a vital process, which means that the plant exercises some control over it. If water is abundant, more will be transpired under a given set of physical conditions than if little water is available. Even Von Höhnel (*100*) showed that ash transpired about 100 kg per 100 g of leaf mass in a unit of time when it was well watered and only 56 kg when lightly watered.

It is also difficult to determine the water requirement of forest trees, since the dry weight at the beginning of the test can be determined only indirectly. In annual crops the weight of seed is taken as the initial weight; but this is not practical in dealing with forest trees, where the early conditions of growth (e. g., in nursery beds) are very different from the later growth conditions. In small potted trees, however, it is possible to estimate the initial dry weight from the green weight.

It has been pointed out above that cut shoots and twigs transpire differently from twigs growing in their normal position. Ivanov (*115*) studied the effect of transpiration by cutting off the shoots of rooted plants and measuring with a stop watch the amount of time it took 5-

to 7-year-old plants to lose a given amount of water. In table 27 are shown the average results of seven trials.

TABLE 27.—*Amount of time required for cut and uncut shoots of young trees to lose ½ gram of water*

Species	Before cutting		After cutting	
	Minutes	*Seconds*	*Minutes*	*Seconds*
Pinus sylvestris	5	42	3	0
Picea excelsa	5	9	1	0
Quercus pedunculata	7	10	3	12

This use of cut twigs to determine the transpiration of whole trees and of stands may even lead at times to ridiculous results. Pfaff (*170*) set himself the task of determining the transpiration of an oak tree from May 18 to October 24 by determining the water losses for 3 minutes from branches removed at regular intervals during this period. The branches were removed from the north side of the tree four different times a day (6 a. m., 11 a. m., 4 p. m., and 9 p. m.) for each of the 160 days. He found that the night transpiration was one-half to one-third that of the daytime and transpiration in the sun three and one-half times that in the shade. Calculating the total number of leaves as about 700,000, he determined that from the unfolding of the leaves until leaf fall the tree transpired 112,100 kg of water. Using the area covered by the crown and that penetrated by the roots as a basis of calculation, in order to give this amount of water 539 cm of precipitation on the area would be necessary. As a matter of fact, the annual precipitation in this locality (Würzburg) is only 65 cm. The oak, therefore, used up in 6 months, according to these theoretical figures, eight and one-half times as much water as fell on the area during the entire year.

To make the matter still more ridiculous, as pointed out by Burgerstein, this figure of 112,100 kg is to be considered only a minimum value because it is calculated entirely on the basis of shade transpiration. If one calculated on a sun basis, the water needs of a tree would be so great that the precipitation during a decade would not suffice to provide the water losses for one growing period.

In the light of these disadvantages and the various problems involved, some of the results obtained by various workers on the actual water needs of economic forest species may be examined. In general all trees seem to thrive better on moist soils; but some are able to tolerate wet or dry soils better than others. Among those that can stand drier soils are certain species of *Betula*, *Populus*, and *Pinus*. *Robinia* can stand much more drought than the nature of its leaves would lead one to expect, and *Fraxinus* also will tolerate dry soils, provided a moderate amount of lime is present. Some species of *Betula* and *Pinus* will also tolerate considerable excess moisture; while most species of *Populus*, *Alnus*, and *Salix* have more than average water requirements.

Turning to specific figures obtained by European workers, among the earliest researchers in this field was Klauprecht, as reported by Morosov (*159, p. 110*), who determined the loss in weight of leaves in the course of a day as measured in percent of their original weight.

According to this early study, the common economic forest species formed the following series:

Species:	*Water loss in percent of fresh weight*
Black alder	43
Oak	37
Beech	36
Birch	29
Larch	18
Fir	12
Pine	11
Spruce	10

Hartig (*88*) measured the loss in weight at regular intervals of potted plants in full foliage, 6 to 8 m high, placed in hermetically closed vessels, calculating the transpiration loss in grams per square meter. He found that, based on transpiration loss per unit area, alder topped the list, heading the following series: Alder>hornbeam>pine>birch >larch>aspen, beech, oak>spruce.

In a later series of experiments (*90*) he found the amount lost in grams per square meter of leaf area was as follows:

	Grams
Black alder	1,250
Hornbeam	290
Pine	255
Birch	217
Larch	206
Aspen	155
Beech	138
Oak	136
Spruce	106

The principal objection to this work is that normal functioning of the roots can hardly be expected in hermetically sealed vessels.

Sorauer (*198*) studied the transpiration of maple, willow, basswood, and pine during 74 days; and Ebermayer, deducing the water loss from the ash content of the leaves, derived the four following groups:

1. Ash content 7 to 10 percent:
   Ash, black alder, maple, elm, poplar.
2. Ash content 4 to 5 percent:
   Beech, oak, hornbeam.
3. Ash content 2.5 to 3.5 percent:
   Larch, fir, spruce.
4. Ash content 1 to 2 percent:
   Pine.

The objection to these latter figures, is of course, the assumption that the ash content varies with the transpiration. While plants that transpire more, probably have a higher ash content, the relation is doubtless not a direct one.

Still another method used by Ebermayer was the determination of the water content of the leaves. In this experiment he obtained the following results (in percent): Poplar, 70; ash, 66; alder and locust, 64; oak, elm, and linden, 63; birch and Norway maple, 62; aspen, beech, hornbeam, and field maple, 57. This method is so unreliable that it was not even considered in the outline given above; as far as one can tell there is no (or little) relation between the water content of the leaves and the water requirements of the plant. Black locust, for example, has a moderately high water content in the leaves but can thrive on relatively dry soil.

Of all the early workers on this subject, Von Höhnel (*98*, *99*) has impressed himself most upon the literature. He used potted trees

5 to 7 years old which were regularly watered and weighed during three entire growing seasons. At least two plants of each species were used, and his calculations were recorded in kilograms of water per 100 g of air-dry weight of leaves per growing season. His average results are given in table 28, column 1.

TABLE 28.—*Average water loss per growing season and per day of potted trees of various species, per 100 grams of air-dry weight of leaves*

Species	Water loss per growing season [1]	Water loss per day [2]	Species	Water loss per growing season [1]	Water loss per day [2]
	Kilograms	*Grams*		*Kilograms*	*Grams*
Fraxinus	85.6	400	*Acer platanoides*	53.1	248
Betula	81.4	380	*Quercus cerris*	45.3	212
Fagus	74.9	350	*Picea excelsa*	13.5	63
Carpinus	73.1	340	*Pinus sylvestris*	9.4	44
Ulmus	66.2	308	*Abies pectinata*	7.0	34
Acer pseudoplatanus	58.6	274	*Pinus laricio*	6.7	31
Quercus pedunculata	53.2	255			

[1] These figures are taken from Horton's (*103*) comprehensive analyses of the work of Von Höhnel.
[2] As calculated by Ebermayer (*55*).

There are several objections to the work of Von Höhnel. In the first place, the vessels contained only about 8 to 12 pounds of soil—a very small amount for trees of that size. Hermetically sealing the pots must also have resulted in unfavorable conditions for the roots, which probably explains the high mortality encountered. Also it has been suggested by Morosov (*159, p. 113*) that the internal temperature of the zinc pots was probably too high. As individual experiments, however, without reference to older trees or larger areas, Von Höhnel's figures agree fairly closely with those of other workers, and Morosov thinks they are still as good as any available.

In the more recent European work Vyssotsky, as given by Morosov (*159, p. 112*), records the following water losses in 1 hour, expressed in percentages of the original weight:

	Percent
Ulmus campestris	19.0
Acer platanoides	10.5
Quercus	9.6
Fraxinus	9.4
Acer campestre	8.0
Pinus sylvestris	2.1
Pinus laricio	.7

The high rate for elm is considered to be due to its thin cuticle.

Huber (*105*) compared the relative transpiration of cut branches; his results are shown in table 29. It must be remembered that the relative transpiration shows the control exercised by the plant over water losses as compared with evaporation from a free (atmometer) surface.

TABLE 29.—*Relative transpiration of cut branches of various tree species*

Species	Transpiration in 1 hour per gram of fresh weight of leaves	Relative transpiration	Species	Transpiration in 1 hour per gram of fresh weight of leaves	Relative transpiration
	Milligrams		*Fagus:*	*Milligrams*	
Betula	190	0.59	Sun leaves	51.5	0.11
Lariz	202	.34	Shade leaves	41.9	.07
Quercus cerris	149	.33	*Picea*	23.5	.15
Q. pedunculata	87.4	.16	*Pinus laricio*	10.7	.06

WATER REQUIREMENT

As to actual water requirement, i. e., number of grams of water utilized by the plant per gram of dry weight increment, very few figures are available for trees. Vater (*219*), in reworking the data of Von Höhnel and Ebermayer, arrived at a figure of 398 for beech, 361 for spruce, and 166 for pine, as characteristic of these three types of forests. Oelkers (*164*) in his recent summary of this subject calculates the water requirements of the common economic species as follows:

Birch	375
Ash	244
Alder	227
Oak	220
Larch	220
Plains pine	213
Beech	209
Mountain pine	208
Spruce	193
Fir	145

In North America the most extensive work in this field has been by Bates and Pearson. Bates (*11*), from potted plants 5 to 6 years old in Colorado, arrived at the following figures as a result of studies over a period of 2 years:

Pinus flexilis	952
Pinus contorta	842
Pinus ponderosa	768
Pinus aristata	743
Pseudotsuga taxifolia	634
Picea engelmanni	456
Pinus sylvestris	436
Larix sibirica	295

Unfortunately, however, only two trees were used in each case. These figures are probably much too large, and it is noteworthy that in 1920 some of his results are less than one-half as large as in 1917. The figures for the last two species mentioned are probably more nearly correct than the others because of the fact that these forms were not studied in 1917.

Furthermore, Pearson (*167*), working with a few of the same species, using potted plants and keeping the soil moisture constant at 20 percent, obtained very much lower results, as indicated in table 30.

TABLE 30.—*Average amounts of water transpired by potted conifers during 2 growing seasons*

Species and number of plants	Age when potted	Dry weight		Transpired, 1919 and 1920	Water used per gram of accretion
		Initial	Accretion, 2 years		
	Years	*Grams*	*Grams*	*Grams*	*Grams*
Bristlecone pine, 6	5	6.54	16.84	7,325	440.0
Yellow pine, 9	4	3.82	23.25	9,153	395.7
Douglas fir, 6	4	9.92	28.34	10,784	381.0
Engelmann spruce, 6	4	7.44	23.42	8,462	359.0

It will be noted that the order, for the most part, is the same as that found by Bates. Of the three genera studied by Pearson, *Pinus* occurs at the lowest elevations and *Picea* at the highest. The annual precipitation increases upward from about 22 inches, where *Pinus*

is found, to 30 inches, where *Picea* occurs, and the temperature falls from 75° to 60° F. (mean maximum during the growing season).

Sperry (*201*) studied the diameter growth and transpiration of various conifers in different sites, but worked chiefly with *Pinus contorta*, *P. ponderosa*, and *Pseudotsuga taxifolia*. The lodgepole pine transpired most and also showed the greatest diameter growth, followed by ponderosa pine and Douglas fir. All transpired most in the site of the lodgepole pine and least in that of the Douglas fir. Sperry therefore concludes that this is also the order of their water requirement. Although the water requirement in its technical sense was not determined, between June 16 and August 25 lodgepole pine transpired 0.120 cc per gram of green leaf per hour; ponderosa pine, 0.091 cc; and Douglas fir, 0.066 cc. The order is thus seen to be the same as that determined by Bates. Furthermore, as might be expected, ponderosa pine fluctuated less in the other two sites than did the other two species when transferred to the other sites.

When one tries to transfer the water requirement for a given species, as based on pot or individual experiments, to mature stands, numerous difficulties are encountered, as mentioned above, but Von Höhnel attempted to calculate the annual consumption of water of a hectare of a closed stand in terms of inches of rainfall over the crop area. He arrived at the figures of 233 mm for a beech stand 50 to 60 years old and 272 mm for a stand 115 years old.

According to Vater (*219*) the annual increment of beech and spruce on site class II and of pine on site class I are about equal (7,000 kg), as based on the somewhat unreliable data of Ebermayer. He thus computed an annual consumption of water per hectare of 290 mm for beech, 255 mm for spruce, and 103 mm for pine.

Bürger (*24*) shows that while spruce seems to transpire one-fifth as much as beech, when one calculates the weight and size of the needles, number of trees in the stand, etc., the loss from a given timbered area is about the same. Based upon the fact that beech produces per hectare 5,000 kg of dry substance and spruce 5,700 kg, the spruce may actually use more water per year than the beech; and Bürger came to the conclusion that the water needs, expressed in terms of millimeters of precipitation, are approximately the same for these two species. More precisely, his figures are 210 mm of water for beech, 170 to 180 for spruce, 120 for oak, and 47 for pine.

Copeland (*38*), who computed the transpiration for the chaparral of California, came to the conclusion that while *Ceanothus* transpires annually enough water to cover an area equal to that of its entire leaf surface to a depth of 2 feet, *Quercus vaccinifolia* Kellogg and *Castanopsis* transpire only half that amount. He suggested that it might be advantageous to replace one group of species with the other if possible.

Various other workers have tried to compute the amount of precipitation water for various stands and areas. Among these might be mentioned the work of Anders (*4*) on elm, Vogel (*221*) on oak and spruce, Von Höhnel (*98*, *99*) on beech, and Hartig (*91*) on the common economic species of Germany. Attention has already been called, however, to the difficulties and errors involved in such calculations.

Also, as has been mentioned above, many difficulties are encountered in transferring values from pot experiments to the field, particularly in the calculation of transpiration. What is the area of the leaf surface of a stand? Illick and Aughanbaugh (*113*) calculated that

northern white pine has about 19 acres of leaf surface per timbered acre and pitch pine about 7.6 acres. Tiren (*214*) calculated that Scotch pine has about 8 acres of leaves per acre of woods, and Zon (*249*) agrees that 8 acres is an average figure. On this basis, an average stand would transpire about ½ to 2½ inches of rainfall per month, according to the figures of Bates (*11*). With a growing season of 5 months and (assuming) a low transpiration for the other 7 months, there would then be need for at least 2 to 12 inches of rainfall a year, a figure which agrees fairly well with those of European workers in forests of equal density. The species used by Bates are characteristic of dry, open sites, especially the pines; and, according to Baker (*6, p. 59*), there are certainly less than 8 acres of leaf surface per acre of limber pine and bristlecone pine forest.

Since plants can maintain themselves on less water than they use when it is plentiful, one should also keep in mind that (1) average forests of the Rocky Mountains doubtless use amounts of water nearer the lower values than the higher and (2) favorable site classes produce a given increment more rapidly than poorer ones.

Age of trees also must be taken into account. The studies of Weber (*232, p. 156*) indicate that an increment of 1 foot board measure per acre per year means an increment of about 15 pounds, including branches, roots, leaves, etc. On this basis the water consumed annually would vary between wide limits, as computed by Baker (*6, p. 61*) and indicated in table 31.

TABLE 31.—*Annual water utilization of western American conifers in stands of varying growth rate, ranging from open arid to dense and very productive, based on average water requirement*

Annual increment		Mean water requirement	Water per acre	Surface precipitation
Feet, board measure	Pounds			
			Pounds	*Inches*
50	750	560	420,000	1.77
100	1,500	560	840,000	3.54
200	3,000	560	1,680,000	7.08
500	7,500	560	4,200,000	17.70
1,000	15,000	560	8,400,000	35.40

For average mesophytic species the annual use of water would be 5 to 15 inches, which agrees very well with the figures obtained by the methods previously discussed. If we took the averages of the precipitation water as calculated by Von Höhnel, Vater, and Burger, we should probably come to a figure not far wrong. Such a method of calculation would indicate the minimum amount of precipitation water used by the various types of forest species to be somewhat as follows:

More xerophytic conifers (pines) ..... 75 mm (about 3 inches)
More xerophytic hardwoods (oaks) ..... 120 mm (about 5 inches)
More mesophytic conifers (spruces) ..... 215 mm (about 8.5 inches)
More mesophytic hardwoods (beech) ..... 260 mm (about 10 inches)

These figures agree very closely with those of Baker (*6, pp. 57–59*), who considers that the water requirement of trees averages about 300

and that the mesophytic hardwoods use up 8 to 11 inches of water per year, the less xerophytic conifers 7 to 10 inches, and the more xerophytic conifers 2 to 4 inches.

Minckler (*153*) calculated that an American elm with a diameter breast high of 13 inches transpired 8.7 liters of water a day. With a growing season of 150 days and 375 trees to the acre, this is equivalent to 4.8 inches of rainfall. A red maple, however, growing in a very moist habitat transpired 51.7 liters daily. This is 7,775 liters for the growing season, and again assuming 375 trees to the acre it equals 28.3 inches of rainfall per acre. It must be recalled, however, that this latter figure is a maximum, under favorable conditions, and does not indicate the minimum requirement; such semihydrophytes would probably need nearer 30 than 20 inches of annual rainfall as a minimum.

This is in agreement with the computations of Horton (*103*) who, basing his calculations on the transpiration data of Von Höhnel, computed the weight of leaf tissue in stands of various species, ages, sites, and densities. He thus calculated that 60-year-old even-aged full-stocked stands would have the following maximum seasonal transpiration:

	Maximum transpiration, inches per acre
Douglas fir	7.67
White pine	8.06
Red spruce	22.95
Hickory	9.90
Beech	25.68

These figures are considerably higher than the previous ones because they represent maximum and not minimum demands.

The precipitation water consumed by trees, however, does not include all of the precipitation. A certain proportion of the precipitation remains suspended in the crown and a certain other proportion evaporates from the soil and surface vegetation or runs off and is unavailable to the forest stand. According to forest meteorological measurements, probably not more than 40 to 50 percent of the total annual precipitation is available to forests. Assuming that only one-half of the total annual precipitation is available to a forest stand, it is seen that pines cannot be expected to grow where there is an annual precipitation less than 6 inches; oak, 10 inches; spruce, 17 inches; and the more mesophytic hardwoods, 20 inches.

If 50 percent were added to these figures such trees might be expected with a reasonable degree of certainty not merely to survive but also to thrive, other site factors being favorable:

	Annual precipitation, inches
The more xerophytic conifers	9
The more xerophytic hardwoods	15
The more mesophytic conifers	25
The more mesophytic hardwoods	30

The conifers may consequently be expected to survive with 9 to 25 inches of annual rainfall, depending on the species, while commercial hardwoods cannot be grown easily on less than 15 to 30 inches. These figures agree well with the known distribution of forests in the North Temperate Zone and elsewhere, and, on this basis seem fairly reliable. Even in sections such as the southwestern United States where temperature and humidity conditions are somewhat extreme,

Pearson (*168*) reports that piñon-juniper woodland associations occur in regions of 16.5 inches annual precipitation, ponderosa pine in regions of 21.35 inches annual precipitation, and Douglas fir where the annual precipitation is 26.36 inches.

In connection with this question of the minimum amount of water necessary for the growing of trees, it must be borne in mind that, aside from total amounts, one must consider also the seasonal distribution and the humidity. Thus Mayr (*150, p. 26*) states that in the Temperate Zone there must be at least 2 inches of rain in the 4 months of the growing season (May to August) for forests to exist. This is the absolute minimum and even then forests are established naturally with this amount of rainfall only if the humidity is over 50 percent. Regions with 2 to 4 inches of rainfall during the growing period and a relative humidity under 50 percent, e. g. prairies and steppes, have no natural forests but can be forested if special care is taken during the establishment of the stand. Once established they can "make their own climate", in his opinion. If the precipitation is less than 2 inches during these 4 months, no forests can be established, no matter how high the humidity, since the seedlings will always dry out; and with over 4 inches of rainfall during this period, trees will grow, no matter how low the humidity. Any species can grow at 70 percent humidity and with 4 inches of rainfall during these 4 months.

Also the "effectiveness" of the precipitation must be considered, as has been pointed out recently by Bowman (*18*), who, in considering the shelterbelt project in the western United States, called attention to the fact that it is important to know not only the average annual rainfall but also its distribution over a period of time. Five dry years in succession have a far different effect upon the establishment of tree plantings than 5 dry years in regular alternation with 5 wet years. Bowman also emphasized the fact that a generalized rainfall map tells very little about the rainfall effectiveness in any given locality. In establishing a plantation in any particular region, it is extremely important to know not only the general precipitation characteristics but the specific ones for the given region. In other words, rainfall must be interpreted in detail in terms of plant physiology and the forest-crop potential under a wide variety of conditions.

SUMMARY AND SUGGESTIONS FOR RESEARCH

The fundamental problem for the silviculturist—the minimum amount of water necessary for the production of his crop—still remains to be solved. While this probably varies between 6 and 20 inches of rainfall annually, depending upon the species and other factors, a clear-cut answer to this question cannot yet be given. The many factors which must be considered in solving this general problem have been reviewed; some of the methods of approach to the problem and the sources of error have been examined; and also some of the criteria by which critical judgments may be reached concerning solutions have been offered. Even a casual consideration of this subject, however, will leave one convinced that much work still remains to be done.

Since the effectiveness of a given amount of rainfall depends, as has been pointed out before, upon the months in which it falls, the temperature, the relative humidity, the degree of windiness, etc., it is

extremely important to have a detailed correlation of the known growth curves in the local and introduced tree species with the various climatic data in as many localities as possible, if success in establishing forest plantings is to be achieved. Furthermore, the growing importance attaching to the consumptive use of water by trees and other natural vegetation in the economy of many farms and watersheds in the drier portions of the country emphasizes the need for quantitative data. Much more work on the water requirements of trees of all ages and under varying site conditions is needed, since comparatively very little work has been done in this field, and much of this has been purely empirical—a method always wasteful and with little to recommend it, although perhaps necessary in the development of a subject.

More comprehensive studies on large trees are especially desirable. The work from small trees and cut twigs is very unreliable, as has been shown. Work in large portable greenhouses should be planned so that it would be possible to control the environmental conditions and to learn the water requirements at different ages and in different artificial sites which simulate the natural ones. This means apparatus that will permit a careful measurement of both the intake and the output. The fact that trees are large and not easy to handle in experimental apparatus increases the difficulties, but they should not be insurmountable; for no really satisfactory results can be expected until more data are obtained on forest trees and stands under natural conditions, supplemented by laboratory work on a scale comparable with the size of the problem involved.

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